Depth distribution of *Calanus finmarchicus* and *C. glacialis* in relation to environmental conditions in the Barents Sea

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Stage composition and vertical distribution of copepodids of *Calanus finmarchicus* and *C. glacialis* are described during spring and summer in Atlantic and Arctic waters, respectively. The two species co-occurred in the region of the Polar Front, both in moderate to high population densities. Ontogenetic migration, meaning that the migration range becomes progressively wider with advancing stage, was found in both species. The present study also revealed that *C. finmarchicus* had modifications in its ontogenetic vertical distribution. The standing crop of phytoplankton, predominantly *Phaeocystis pouchetii*, appeared to influence the degree of stage-specific segregation. Both low and high food concentrations tended to increase the vertical distribution of the instars. On the other hand, a narrow subsurface stratum of abundant phytoplankton led to an aggregation of copepodids at this depth. In the region of the Polar Front, where the two species co-occur, *C. glacialis* had a deeper distribution than *C. finmarchicus*, thus creating a bimodal vertical distribution pattern within the uppermost 200 m.

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Introduction

There is a tendency in pelagic environments for zooplankton and its food supply to be patchily distributed on any spatial or temporal scale (Dagg 1977). Aggregations of zooplankton have been found on horizontal scales of 1–10 km (Kiørboe 1988), while zooplankton layers, varying in thickness from a few to tens of metres have been observed vertically (Vinogradov 1968; Longhurst 1976). The difference in scales is related to the fact that hydro-dynamic and biological variations in the environment are usually greater when considered vertically than when considered horizontally.

Vertical migration and distribution of zooplankton organisms have been the subject of extensive research efforts since the 19th century (Hardy 1971). In the debate concerning this phenomenon, it has been postulated that the explanations have to be considered at two levels (see Vinogradov 1970; Bohrer 1980; Ringelberg 1980). The phenomenon can, from an evolutionary perspective, be regarded as an adaption to the planktonic way of life (ultimate and teleological mechanisms). On the other hand there is the direct response of the individual, both to environmental and endogenous factors. These can be regarded as the instant and directly acting agents (proximate or causal mechanisms).

Most studies concerning vertical zooplankton migrations have been carried out in temperate regions, where the annual variations in the light and temperature regimes are minor, as compared to polar regions. Consequently, the main topics of these studies have been related to diel vertical migrations. In high-latitude systems, which exhibit pronounced seasonal variations in day-length and temperatures, seasonal and ontogenetic vertical migrations are important features of the vertical migration pattern (Bogorov 1946; Longhurst 1976; Buchanan & Haney 1980; Grøndahl & Hernroth 1986; Eilertsen et al. 1989).

The present study is based on an investigation of the vertical distributions of different developmental stages of the calanoid copepod *Calanus finmarchicus* carried out in 1986 in fjords of northern Norway (Tande 1988). The study from these inshore waters clearly points out that *C. finmarchicus* in this region exhibited both diel and ontogenetic vertical migrations during the spring and early summer. Differences in the vertical

distributions of the copepodids were related to differences in environmental conditions (i.e. temperature and phytoplankton abundance) and in population densities of *C. finmarchicus* between the locations. The study suggested that the vertical separation could be an important mechanism in reducing the competitive interactions among the copepodids of *C. finmarchicus*. Based on samples taken at three time periods in May, the response of the different developmental stages to the environmental conditions was found to be continuously modified throughout the most intensive growth and recruitment period of *C. finmarchicus*.

This complex behaviour pattern of *C. finmarchicus* in inshore waters could have been mediated by local environmental factors such as topography and tidal action. Therefore, the potential effect of hydrographic variability of coastal water might have obscured the behaviourally copepod-generated distribution pattern. Thus, in order to readdress this question specifically related to the vertical behaviour of *C. finmarchicus* in an anticipated more homogeneous physical environment, a new study was undertaken in offshore waters in the Barents Sea. The time period selected in May and June is considered to be the period of culmination of the spring bloom in Atlantic waters (Tande 1991 this volume). Thus it is likely that the herbivorous zooplankton grazing balances the carbon production at least in certain areas (Tande & Slagstad 1991). It is expected that the copepod community displays a vertical distribution pattern that leads to an optimal utilisation of the standing stock of phytoplankton (see Lane 1975; Bohrer 1980; Williams & Conway 1980; Tande 1988). The present study was undertaken in order to describe the vertical distribution of *C. finmarchicus* in different vertically structured phytoplankton environments; it aimed at delineating any consistent pattern between the vertical distribution of *C. finmarchicus* and the physical and biological environment. The area selected was a transect from 73°N to 75° 30'N in the western part of the Barents Sea. The area was sampled twice in the period from 26 May to 13 June 1987, corresponding to the same biological period, and with exactly the same methodological approach as the preceding year in inshore waters in northern Norway.

Materials and methods

Sampling programme

Sampling was accomplished during a survey with R/V ENDRE DYRØY, from 26 May to 13 June 1987. A series of 3 stations along a transect between 73°00'N 28°00'E and 75°30'N 30°00'E was taken at the start of the cruise and was repeated at approximately the same locations (except for Stations 6 and 17) at the end of the cruise 14 days later (see Table 1 and Fig. 1). Station time varied slightly, but most of the collections were carried out between 0830 and 1400 CET (Central European Time), except at Station 1 (1100–1910 CET).

Hydrography and light conditions

Conductivity, temperature and density measurements (CTD) were performed using a Neil Brown Instruments Smart CTD coupled to a Hewlett-Packard computer. In order to construct the isoplots in Fig. 2, hydrographic measurements from stations at 73°30'N 28°00'E and 74°30'N 30°00'E were used, in addition to the sampling stations shown in Fig. 1. Since surface irradiance is

Table 1. Timing, position, weather and depth data for the different sampling stations (Stn.). Wind speeds were measured at start of sampling.

Stn.	Date	Time (CET)	Position	Cloudiness (%)	Depth (m)	Wind (m/s)
1	26.05	1100–1910	73°00'N 28°00'E	90–100	333	4.6
3	28.05	0845–1400	74°00'N 28°00'E	100	402	9.8
6	31.05	0850–1355	74°30'N 30°00'E	90–100	365	1.0
13	09.06	0840–1405	73°00'N 28°00'E	100	333	4.6
15	11.06	0830–1325	74°00'N 28°00'E	100	402	4.6
17	13.06	0840–1315	75°00'N 30°00'E	100	387	9.8

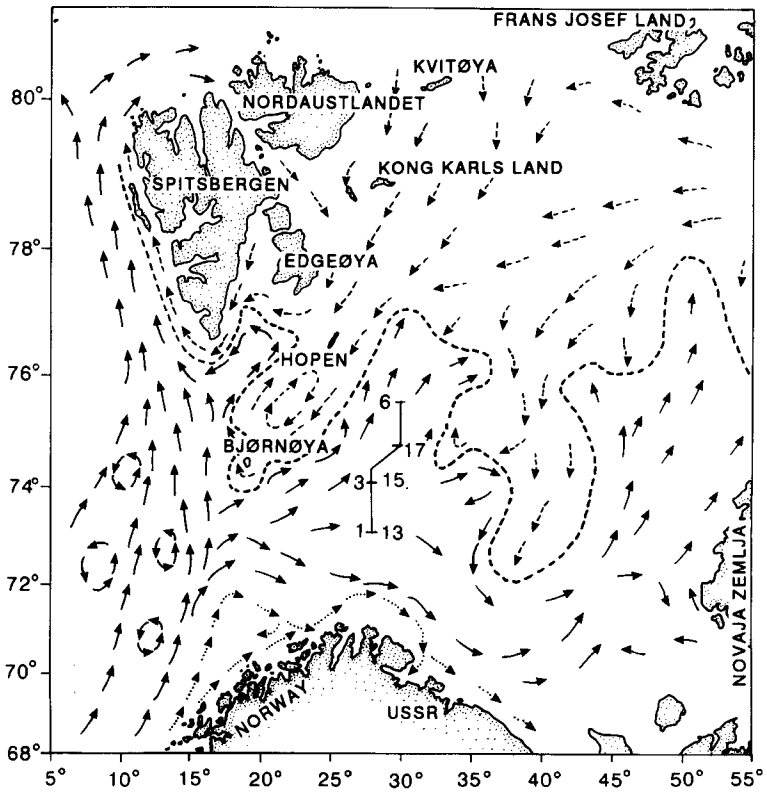

Fig. 1. Map of the Barents Sea showing the investigated area and the sampling stations (1–17). Also shown are the average position of the Polar Front (stippled line) and the surface currents: Arctic currents (broken arrows), Atlantic currents (solid arrows) and coastal currents (stippled arrows). After Midttun & Loeng (1987).

approximately inversely proportional to cloud coverage (Kuz'min 1972), data for the latter were used to detect major differences in the light regimes of the sampling locations.

Plankton

Zooplankton was sampled by means of a pump system (see Solemdal & Ellertsen 1984) which consists of a 90° bent glass fibre tube with a diameter of 40 cm. A plankton net (180 μm mesh) was mounted on the vertically-oriented outlet while the impeller was positioned on the horizontally oriented opening. Samples were taken at discrete depths from the surface down to a depth of 195 m, at 15 m intervals. No sampling from the deeper water masses was carried out. Pumping time was set to 6 minutes and water flow was measured with a TSK (Tsurumi-Seiko-Kosha-kusho Co. Ltd.) flowmeter. The flow rate varied, probably related to the position of the pump relative to the currents, and the values typically varied between 5 and 10 $m^3 min^{-1}$.

For the collection of phytoplankton, a 5 liter. Niskin water bottle was mounted externally on the pump. The closing mechanism was remotely controlled by the power source of the pump in such a way that the bottle was closed at the initiation of pumping. Both zoo- and phytoplankton samples were preserved in 2% formaldehyde in seawater, buffered with borax. 50% (by volume) 1.5 propane diol, which functions as a bacteriacide that also helps keeping setae and appendages soft, was added to the zooplankton conservation medium.

In the laboratory, the *Calanus* specimens were identified and counted using a Wild M3 stereo microscope at either 16 or 40× magnification, depending on copepod size. The different stages of *Calanus* spp. were assigned to species using the prosome lengths given in Table 2. Samples containing large numbers of copepods were split into ten using a Lea-Wiborg splitter (Wiborg 1951). The number of fractions analysed was adjusted so that 50 or more were counted for each copepodid stage. This procedure gives an estimated value that deviates by less than 30% from the real sample size (Aksnes 1981). From the

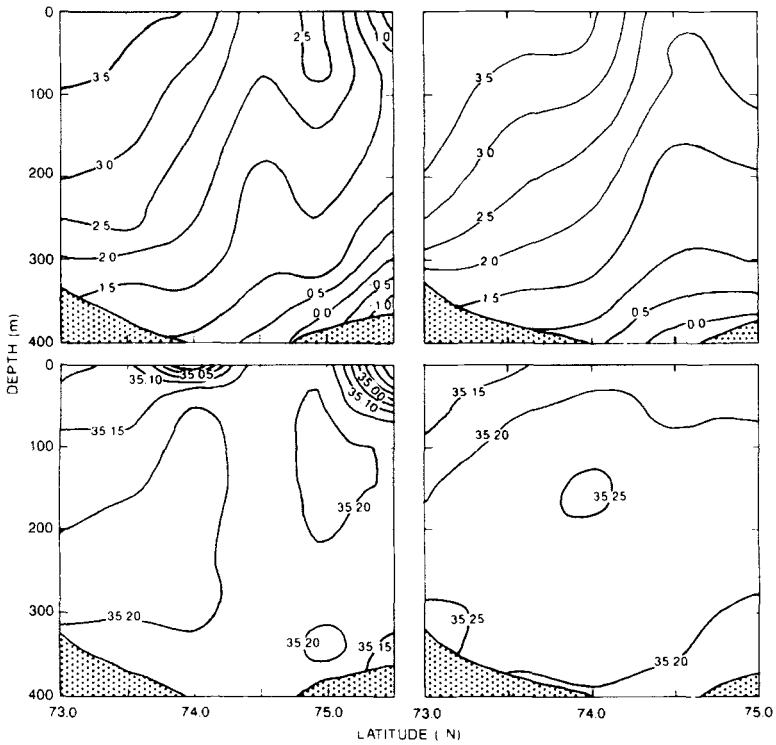

Fig. 2. Isoplots showing temperature (upper) and salinity (lower) for series 1 (left) and series 2 (right), respectively.

resulting copepod densities, the total population size could be estimated by simple plane integration. Phytoplankton was identified and counted from duplicate subsamples, according to the method described by Utermöhl (1958). During this process a Wild Heerbrugg inverted microscope was used at 200× magnification.

Results

Hydrography and phytoplankton

There was a general decrease in temperature going northwards in the area of investigation in both of the series (Fig. 2). No thermal stratification was seen, except for the most northern area at 75.5°N in series 1 (Station 6). Isotherms show that temperatures generally decreased between 0.5 and 1.0°C from surface down to a depth of 195 m, in such a way that the differences in surface values between areas tended to persist down to the deepest depth of sampling. Salinity showed little temporal and spatial variation, ranging from 35.15 to 35.25‰. A decrease in salinity was found in two regions at 74°N (Station 3) and 75.5°N (Station 6) in series 1, respectively, with low surface salinities (<35.00‰) due to meltwater from sea ice.

The phytoplankton communities of all sampling locations were dominated by the prymnesiophyte *Phaoecystis pouchetii*. Although other phytoplankton groups were present, the degree of dominance of *P. pouchetii* was so high that this species was considered as representative of the food avail-

Table 2. Calanus spp. Identification key for *C. finmarchicus* (CFIN), *C. glacialis* (CGLA) and *C. hyperboreus* (CHYP). Modified from Hassel (unpubl.).

	Prosome length (mm)		
Stage	CFIN	CGLA	CHYP
CI	<0.85	0.85–0.90	>0.90
CII	<1.20	1.20–1.42	>1.42
CIII	<1.65	1.65–2.15	>2.15
CIV	<2.30	2.30–3.00	>3.00
CV	<3.00	3.00–3.40	>3.40
Females	<3.20	3.20–4.50	>4.50

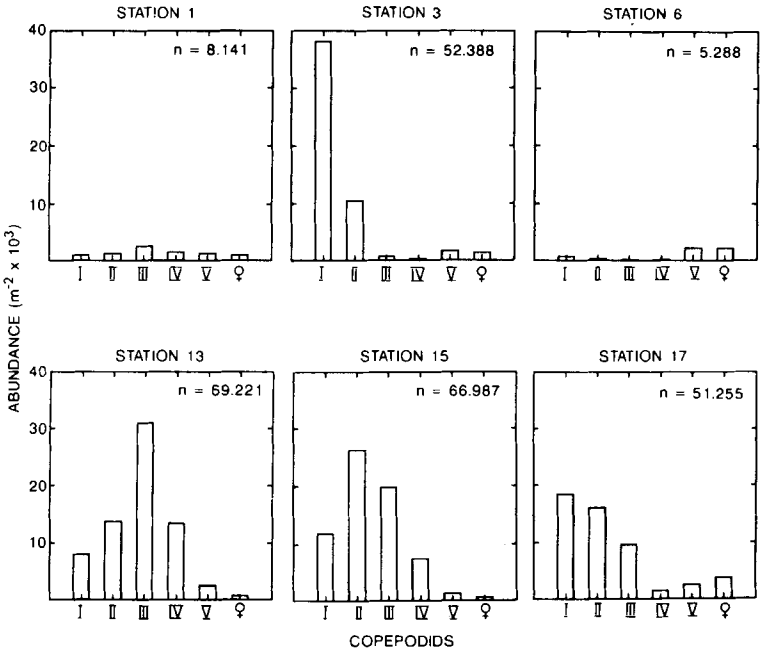

Fig. 3. Calanus finmarchicus. Stage composition at all stations in the two series.

able for the copepods. Therefore, the phytoplankton conditions will be described here with respect to *P. pouchetii* only.

As shown in Table 2, the mean values for cloud coverage varied between 90 and 100%. Thus no great differences in light conditions between the stations could have been caused by variability in cloudness.

Calanus finmarchicus: temperature, phytoplankton, and vertical distribution of copepodids.

Series 1. – In the first series, Station 1 exhibited the highest sea surface temperature (3.6°C) compared to the other two stations further north (Fig. 4). The abundance of *P. pouchetii* varied greatly between Stations 1, 3 and 6. At station 1, the lowest phytoplankton standing stock was found. The number of *P. pouchetii* was highest at 30 m depth, with 1.27×10^6 cells l^{-1}. Below this depth, cell numbers were low. The copepodite stages in the population of *C. finmarchicus* at Station 1 were represented in relatively equal proportions (see Fig. 3 for stage composition). However, the population, which was estimated to a total size of 8141 individuals m^{-2}, contained a somewhat higher proportion (30.2%) of CIII. The depth of maximum occurrence increased with each stage (Fig. 4): CI and CII had their highest numbers at 45 m, CIII at 60 m, and CIV and CV at 75 m and 165 m, respectively. The adult females were most numerous at 180 m.

At Station 3 the surface temperature was approximately 3.4°C, steadily decreasing to 2.2°C at 200 m depth. The phytoplankton peaked at 75 m of depth, with maximum in *P. pouchetii* of 2.37×10^6 cells l^{-1}. The copepod abundance and stage composition was clearly different from Station 1: CI made up 73% and thus totally dominated in the population of 52,000 individuals m^{-2}. The vertical distribution pattern was almost similar to that at Station 1, except for the tendency of CV and adult females to occupy a shallower depth (see Fig. 4).

At the northernmost station (Station 6) the vertical temperature profile was characterised by cold surface water overlying deeper water masses with a temperature of approximately 1.2°C. The bulk of phytoplankton was found between the surface and a depth of 60 m, where the cell numbers peaked at 30 m with 10.4×10^6 cells l^{-1}. Here, *C. finmarchicus* was found at the lowest abundances recorded during the investigation (5300 individuals m^{-2}). A bimodal stage distribution was seen in which the population consisted of primarily CV and adult females (see

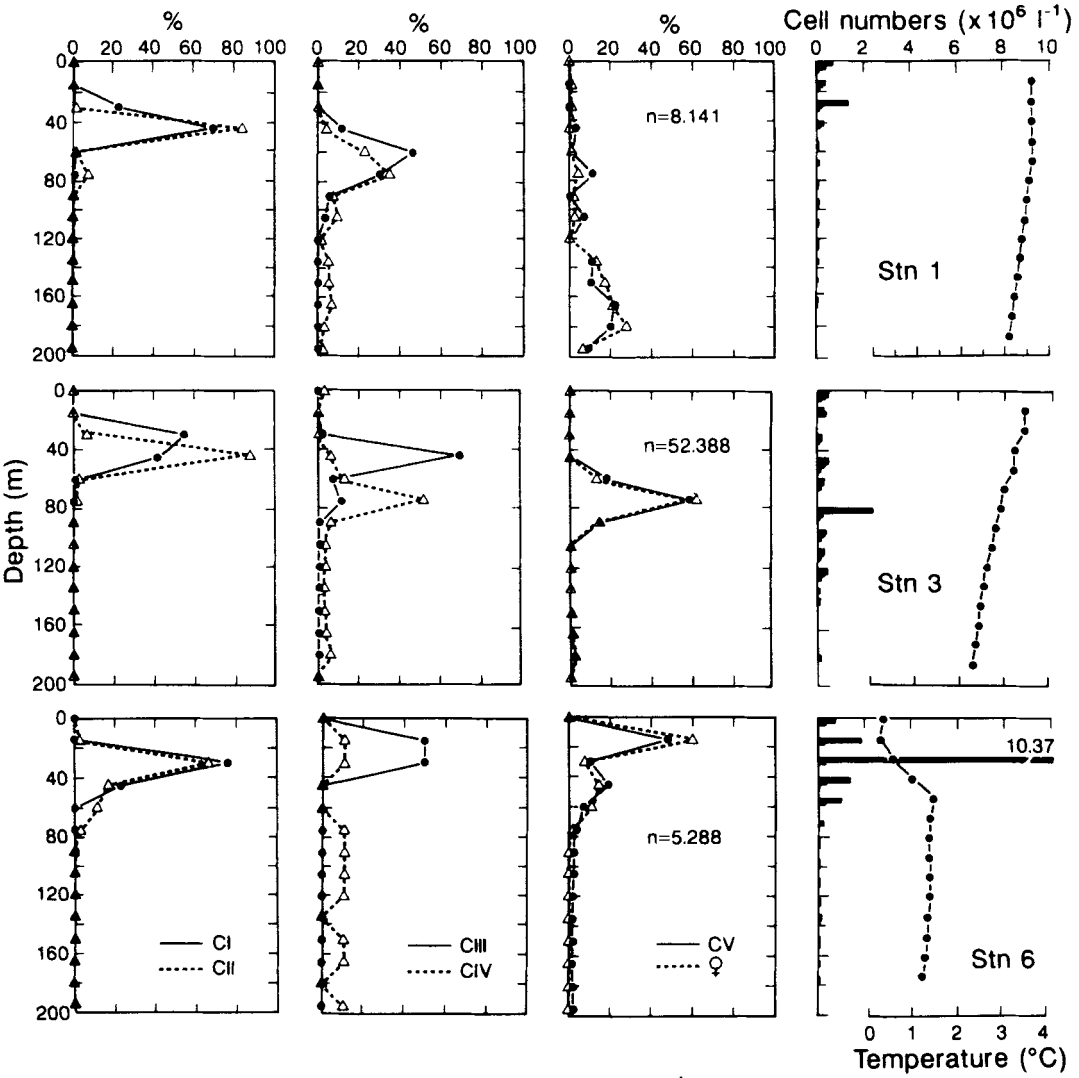

Fig. 4. Vertical distributions of *Calanus finmarchicus* and *Phaocystis pouchetii* cell numbers, together with temperature profiles at Stations 1, 3 and 6.

Fig. 3), in addition to a lesser proportion of the smallest copepodids (CI and CIII). Vertically, CI and CII had their highest numbers at 30 and 45 m, respectively, thus resembling the population distributions at Stations 1 and 3 (Fig. 4). In contrast to all the other sampling locations, the two most advanced instars occupied shallower depths and had a depth of maximum occurrence at 30 m.

Series 2. – Sampling of the same area two weeks later showed a temperature in the upper water layers which was in general higher than that found at corresponding locations in series 1. At Station 13 a surface temperature of 3.9°C decreased slightly with depth (Fig. 5). The phytoplankton was present at notably abundances only in the uppermost 45 m of depth. The highest abundance of copepodids throughout the whole survey was found at this station (62,000 individuals m^{-2}). CIII dominated with 45% of the total population. CII and CIV were each represented by almost 20%, while CI constituted the smallest proportion of the population (see Fig. 3). A clear ontogenetic vertical distribution was seen, with the majority of the entire population found below the surface maximum in cell numbers (Fig. 5).

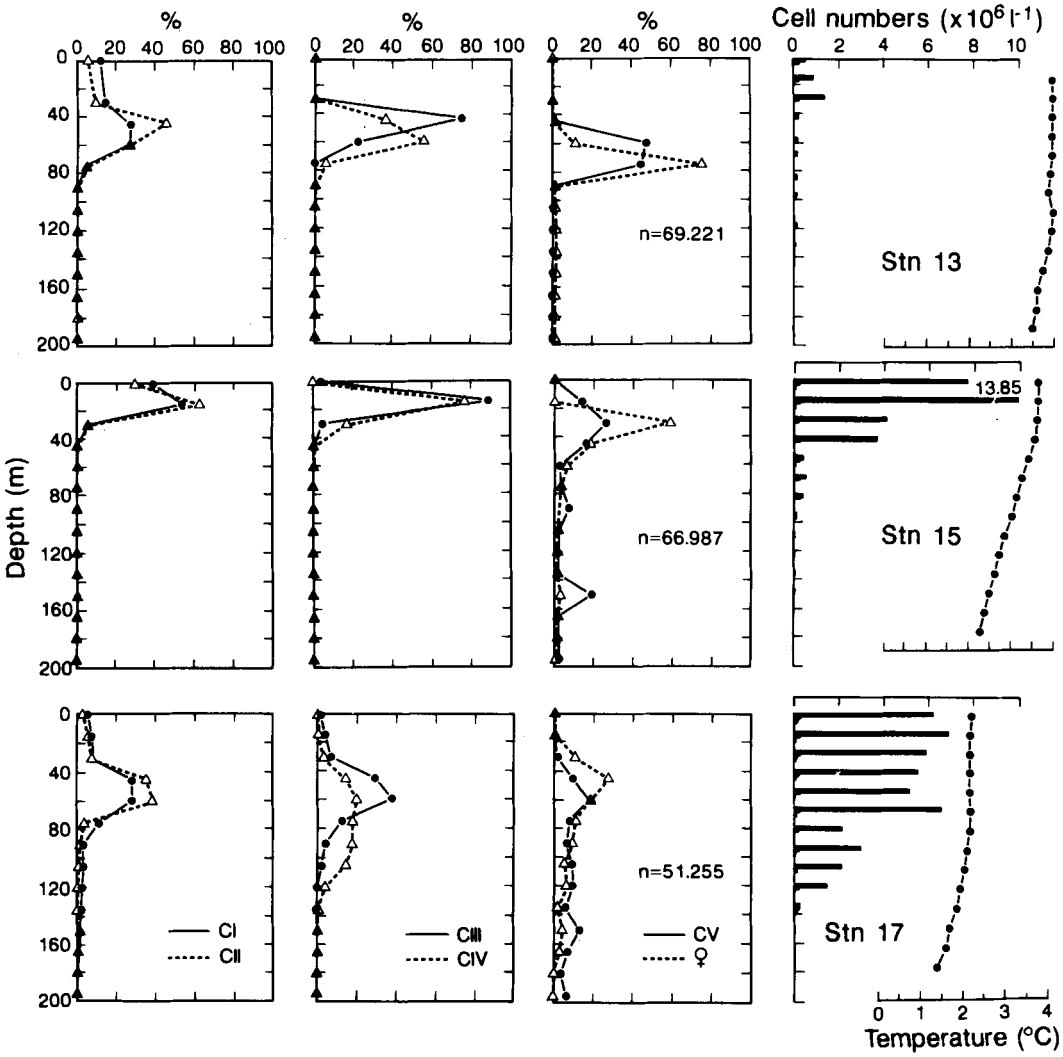

Fig. 5. Vertical distributions of *Calanus finmarchicus* and *Phaocystis pouchetii* cell numbers, together with temperature profiles at Stations 13, 15 and 17.

A surface temperature of 3.6°C was found at Station 15, with a slightly more pronounced vertically decrease in temperature compared to the former location. The phytoplankton was found in very high abundance in the uppermost waters, where *Phaeocystis pouchetii* peaked in maximum abundance (13.9×10^6 cells l^{-1}) at 15 m of depth. The total abundance of *Calanus finmarchicus* was found at about the same size as that at Station 13 (Fig. 3). The majority of the population appeared as CII, CIII and CIV, and was located in the uppermost 45 m of depth.

At the northernmost station surface temperatures were approximately 2°C, and decreased to 1.3°C at 170 m (Fig. 5). The greatest standing crop ever recorded during the investigation was found at cell densities of approximately 6×10^6 l^{-1} in the uppermost 60 m of depth. The abundance of *C. finmarchicus* was relatively high also at Station 17. Out of a population of 51,300 individuals m^{-2} (Fig. 3), CI and CII made up 36 and 31%, respectively, and thus constituted the largest proportion of the population. Relatively low abundance of CIV and moderately high numbers of CV and adult females resulted in a bimodal stage-distribution pattern at Station 17, a situation

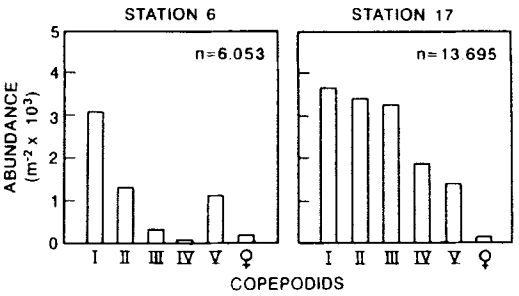

Fig. 6. Calánus glacialis. Stage composition at Stations 6 and 17.

which also was seen at Stations 6 and 3. The various stages were distributed vertically from 40 to 80 m of depth, although with a tendency for a larger vertical spread, especially pronounced among CV and adult females (see Fig. 5).

Calanus glacialis: temperature, phytoplankton and vertical distribution of copepodids.

Calanus glacialis was abundant only at the two northernmost sampling locations, Stations 6 and 13 (see Figs. 6 and 7). The following information in the data set is emphasised:

At Station 6, *C. glacialis* was present in low numbers, estimated at 6053 m^{-2}. The population was composed mainly of two groups of instars, the majority of which were copepodid Stages I and II, representing 50.9 and 21.7%, respectively. CV, which constituted 18.2%, made up the second group. The two early copepodite Stages (CI and CII) were found between 30 and 90 m, while the more advanced stages displayed a wider depth distribution, having been recorded at depths between 30 and 105 m (Fig. 7). Low numbers of CV and adult females were found at all depths, except for a peak in distribution at 30 m, which was somewhat shallower than the younger stages.

Samples taken two weeks later and 30 nautical miles further south (Station 17) contained greater amounts of *Calanus glacialis* and the total population size was estimated to 13.695 individuals m^{-2} by plane integration. Of this, the first three copepodite stages made up more than 75% (26.6 CI, 24.9% CII and 23.7% CIII), while the rest of the population was mainly composed of

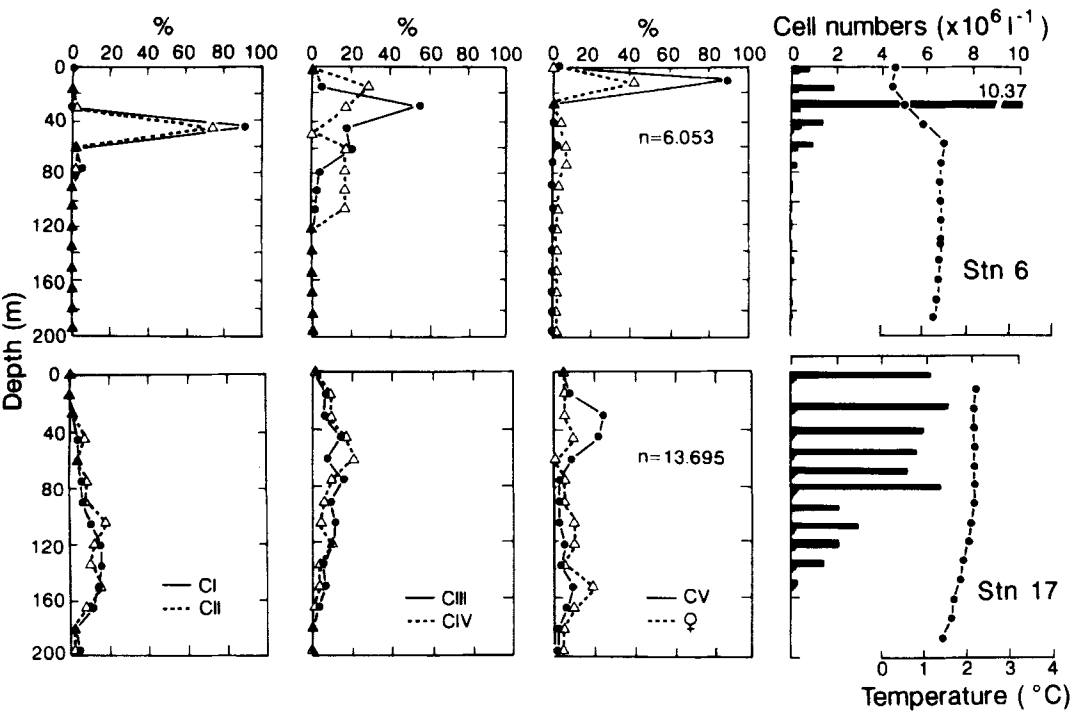

Fig. 7. Vertical distributions of *Calanus glacialis* and *Phaocystis pouchetii* cell numbers, together with temperature profiles at Stations 6 and 17.

copepodids in Stages IV and V. At Station 17, all the copepodid stages of *C. glacialis* were recorded at all sampled depths (Fig. 7). The tendency for successively larger stages to have shallower depths of maximum occurrence, as could partly be seen at Station 6, was clearly evident at Station 17. A tendency towards a bimodal depth distribution was also seen, especially in copepodite stage V.

Correlation analysis

A correlation analysis was performed on untransformed depth values of the numbers of each developmental stage. The resulting values were then used in a MDS (Multi-Dimensional Scaling) analysis. The spread in coordinates representing depth distributions of the different populations (Fig. 8) is seen mainly along the horizontal axis (dimension). The largest distance is between the coordinates representing depth distributions for *Calanus glacialis* at Station 17 and *C. finmarchicus* at Stations 1 and 6. On the other hand, the coordinates for *C. finmarchicus* at Stations 13, 15 and 17 may be considered to constitute a group. The coordinates representing the vertical distribution pattern of *C. finmarchicus* at Station 15 are segregated from this group, mainly along the vertical axis (dimension 2).

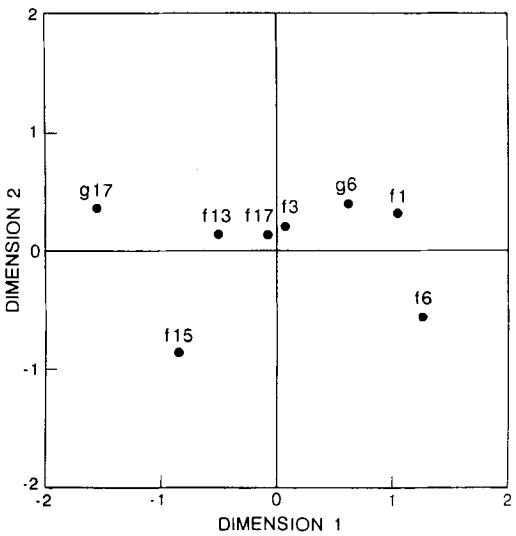

Fig. 8. MDS plot showing coordinates representing the vertical distributions of *Calanus finmarchicus* (f) and *C. glacialis* (g) at the different stations (numbers).

Discussion

Calanus finmarchicus, together with its two sibling species *C. glacialis* and *C. marshallae*, constitutes a group that is distributed over the entire Atlantic north of 40° latitude, and throughout the Barents Sea, the Polar Basin and the northern Pacific (Jaschnov 1961, 1970; Matthews 1969, Fleminger & Kulsemann 1977; Frost 1974). In the Barents Sea, *C. finmarchicus* is mainly found north of the Polar Front area (see Fig. 1), while *C. glacialis* is an indicator species of water masses of Arctic origin and consequently has its main area of distribution north of the Polar Front (see Jaschnov 1961). The area of the present investigation was located in the Atlantic part of the Barents Sea, with the exception of the most northerly area, and *C. finmarchicus* was the dominating copepod species. At the two stations near the Polar Front, *C. glacialis* was present in the same order of magnitude as *C. finmarchicus*.

Length ranges of *C. finmarchicus* and *C. glacialis* have been shown to overlap, and a plasticity in body lengths appears when comparing populations from different regions (Frost 1974). The relatively slight degree of morphological divergence further complicates distinguishing between the two species when analysing zooplankton samples. Length–frequency distributions that were constructed during the analysis of the present material (Unstad unpubl. results) showed that the prosome lengths of copepodids of the two species showed some degree of overlap. Overlapping "tails" of the distributions, however, were considered not to give more than marginal effects in distinguishing the two species when they occurred in equal proportions of abundance. At the same time, the use of prosome lengths would lead to a substantial over-estimation of one species if it was represented by a very small fraction as compared to the other species.

The annual spring bloom in the Barents Sea is characterised by the presence of large amounts of the prymnesiophyte *Phaeocystis pouchetii* (Zenkevich 1963). Although inter-annual variations in species composition appear (E. Nøst-Hegseth pers. comm.), there is a trend towards *Phaeocystis* domination in high latitudes, which is especially pronounced for the period after the culmination of the spring bloom (Eilertsen et al. 1981). In the area of investigation, both population size and vertical distribution of *P. pouchetii* varied and the highest cell numbers were found between depths

of 15 and 60 m. There was also a tendency for the phytoplankton standing crop to be larger at the more northerly locations. The fact that relatively high cell densities were found down towards depths of 150 m indicates that the bloom in the area of investigation was in its culminating phase during this study (H. C. Eilertsen pers. comm.).

Even though the dominance of *Phaeocystis pouchetii* may theoretically have been a consequence of selective grazing by zooplankton upon other phytoplankton taxa, *P. pouchetii* is regarded as the main food source for the herbivorous zooplankton during the research period. Although the trophic fate of this species has been discussed for years, *P. pouchetii* is consumed by *Calanus finmarchicus* and other members of this genus (Turner 1984; Tande & Båmstedt 1987; Hansen et al. 1990b). Huntley et al. (1987) found that *P. pouchetii* alone could sustain the nutrient demands of *C. hyperboreus* in terms of carbon.

In the life cycle of *P. pouchetii*, both small, flagellated solitary cells and colonies comprising non-flagellated cells appear. The colonies are often larger than 200 µm in diameter. According to Hansen et al. (1990b), particles with an equivalent spherical diameter (ESD) of 50 µm are in the upper proportion of the size range of food particles suitable for Stage I–III copepodids of *C. finmarchicus*. During the culmination of the spring bloom, the fraction of disintegrating colonies increases (Hansen et al. 1990b). Colonies in this state may be easier for the small copepodites to consume.

During the period of investigation, the greatest proportion of the *C. finmarchicus* population inhabited depths from 15 to 100 m. Copepodid Stages I and II (CI and CII) were generally found at depths of less than 50 m, while CIII and CIV tended to be located above 120 m depths. CV and adult females generally inhabited the upper 100 m of the water column, but the distributions within this depth interval varied between the stations. At one instance (Station 1), the greatest proportions of CV and adult females were found at depths of nearly 200 m. The deeper limit of vertical distribution can be seen in relation to coexisting copepods; samples from depths greater than 100 m typically contained large amounts of *Metridia* spp. and *Pseudocalanus* spp. (Unstad unpubl.). Low numbers of *Calanus* spp. in the upper 15 m of the water column at all stations except Station 15 may be related to illumination preferences, with light intensities near the surface possibly exceeding the light optimum (see Boden & Kampa 1967) of the animals. No samples were taken from depths greater than 195 m, but as very few copepodites were found in the lower part of the sampled depth range this may indicate that no substantial part of the population was located at greater depths.

The vertical distribution patterns indicate an existence of ontogenetic vertical migration in *C. finmarchicus* at Stations 1, 13, 15 and 17. At these locations, successively older copepodids tended to be located deeper in the water column than the younger developmental stages. No such tendency was found at Station 6, but this locality differed strongly from the other stations in displaying a stratification where the upper part of the water column showed temperatures lower than the rest of the sampled depth interval. Additionally, *C. finmarchicus* co-occurred in relatively low numbers with *C. glacialis* (see below).

The degree of stage-specific segregation seemed to be related to the vertical distribution of phytoplankton biomass and to the relative abundance of food available to the copepods, i.e. phytoplankton biomass versus copepod population size. At Stations 6, 13 and 15, the vertical phytoplankton distributions revealed distinct depth-specific peak levels of algal biomass, and the *C. finmarchicus* populations tended to aggregate in these depth strata. At Station 17, the phytoplankton was vertically dispersed and high cell numbers were found from the surface down to depths of 135 m. At this location the degree of stage-specific segregation was greater than at the previously mentioned stations and the depth stratum inhabited by each stage was wider. At Station 1, where phytoplankton cell numbers were low throughout the sampled depth interval, the vertical dispersion was pronounced. However, this tendency was not as clear at Station 3, even though cell numbers were low also at this location. A small peak in the number of phytoplankton cells at 75 m, together with a high number of copepodid Stages I and II at Station 3, are features that distinguish this station from Station 1. It is difficult to conclude that this might account for the difference in dispersion among instars between the two stations. At this point, the present data set is insufficient and further information is needed.

At Stations 6 and 17, the Arctic species *C. glacialis* was found in the same order of magnitude as the populations of *C. finmarchicus*. At both

stations, CI dominated, but at Station 17, a large proportion of CII–CIV was also found. As for *C. finmarchicus* at these stations, the copepodids of *C. glacialis* displayed a depth distribution with a small degree of overlap between the different stages. The ontogenetic tendencies in the vertical distributions of *C. glacialis* were inverse to those of *C. finmarchicus*, so that the youngest stages of *C. glacialis* were found at depths greater than those where advanced stages were found. This contrasts with the findings of Hansen et al. (1990a), where the older stages of *C. glacialis* were found deeper in the water column than the younger copepodites. However, Williams & Conway (1980) demonstrated an inverse stage-specific vertical distribution in *C. finmarchicus* as compared to the congenric species *C. helgolandicus* in the North Sea and the Celtic Sea, resembling the differences in vertical distributions between *C. finmarchicus* and *C. glacialis* found in the present study. At Station 17, the population of *C. glacialis* was spread more vertically than its sibling species and could be found throughout the whole interval from 15 to 180 m. In this way the bulk of *C. glacialis* had the deeper distribution of the two species, a tendency similar to what was found by Herman (1983) in Baffin Bay. Even though there was less vertical spread between the two *Calanus* species at Station 6, similar differences between the vertical distributions of the two species could also be seen here.

The grouping of the coordinates which represent the vertical distribution patterns of *Calanus finmarchicus* at Stations 3, 13 and 17 by the MDS analysis illustrates their similarity. The increased distance between these points and the coordinate representing the *C. finmarchicus* profile at Station 15 are most likely related to the upward shift in the latter profile, as compared with the three previously mentioned. The position of the coordinate representing the *C. finmarchicus* profile at Station 1 near the ones representing both this species and *C. glacialis* at Station 6 may be due to the relatively low representation of both species at these two stations. The differences in ontogenetic distribution patterns between the two sibling species are reflected by the position of the coordinates representing the two species at Stations 6 and 17 some distance apart from each other. The relatively large distance between the points representing *C. glacialis* at the two stations may be related to the differences in population sizes of this species.

The present study reveals that *C. finmarchicus* showed modifications in its ontogenetic vertical distribution. Both low (Station 1) and high food concentrations (Station 17) appeared to increase the vertical distribution of the instars. On the other hand, a narrow subsurface stratum of abundant phytoplankton led to an aggregation of copepodites at this depth (Stations 6, 13 and 15). The observed shifts in ontogenetic vertical distributions in *C. finmarchicus* in high latitude offshore and inshore (Tande 1988) waters could thus be explained by changes in food availability. Although the present study does not facilitate an examination of alternative causal relationships, similar future studies should encompass the species complexities at the study site, including physical processes and predation. The monitoring of the same body of water for a time period of several weeks is a prerequisite for future investigations of any causal relationships aimed at improving our understanding of vertical behaviour in zooplankton.

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