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# *Calanus* spp. grazing affects egg production and vertical carbon flux (the marginal ice zone and open Barents Sea)

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## Abstract

Concentration of faecal pellets of *Calanus finmarchicus*, *Calanus glacialis*, and *Calanus hyperboreus*, as well as eggs and nauplii of the first two species in the upper 0–100 m layer, were estimated during 24-h stations in the marginal ice zone and the open Barents Sea in March, May, and July. The importance of *Calanus* spp. as major contributors to suspended matter and vertical flux was confirmed, as the proportion of their faecal pellets was high and rather stable in the upper 100 m layer throughout the study period, varying between 48% and 95% of total suspended pellet carbon (maximum dimension >50 μm) and comprising more than 50% of sediment matter. Feeding activity of calanoid copepods was not correlated with the seasonal changes in total phytoplankton carbon, but with assumed preferred food. Egg production was correlated with feeding activity depending on the temporal scales of the study (monthly, daily, hourly). A significant positive correlation between egg and faecal pellet concentration on a monthly scale, a weak significant (*C. finmarchicus*), or, insignificant (*C. glacialis*) positive correlation between daily egg and faecal pellet production, and a significant negative correlation between hourly egg and faecal pellet production (*C. finmarchicus*) were obtained. Significant correlations between indices of current feeding activity (or, available food), egg production and nauplii concentration obtained in the field suggest that current feeding, not lipid reserves, played a major role in supplying the energy for reproduction of *C. finmarchicus* and *C. glacialis*.

*Keywords:* Feeding activity; Egg production; Faecal pellets; *Calanus finmarchicus*; *Calanus glacialis*; *Calanus hyperboreus*; Barents Sea

## 1. Introduction

Three sibling species of calanoid copepods, *Calanus finmarchicus*, *Calanus glacialis*, and *Calanus hyperboreus*, play an essential role in trophodynamics of the pelagic systems of the North Atlantic and adjacent seas. They are recognized as important prey organisms for larvae and juveniles of a number of commercially exploited fish (Kane, 1984; Astthorsson and Gislason, 1997), and it has been suggested that the recruitment in various fish stocks may be related to abundance of these species (Cushing, 1984). *C. finmarchicus* is also the dominant species in the North Atlantic zooplankton biomass (Batchelder et al., 1995).

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The life cycle strategies in copepods of high latitudes are generally adjusted to seasonal changes in phytoplankton abundance. Lipid storage is a part of the normal life cycle of many high-latitude species, including the three related calanid species studied. Following accumulation of lipid reserves, copepods descend to the depth, where they spend the unfavourable winter period, reducing their metabolism (Østvedt, 1955; Hirche, 1996a; Kaartvedt, 1996; and references therein). When they ascend to the surface layers in spring, they have to use the short period of phytoplankton abundance, giving rise to the new generations, and storing energy depots. Presumably, foraging activity should be very high at that period (Pasternak et al., 2001). However, recent studies suggest that feeding, growth and development of *Calanus* sp. is only weakly associated with the abundance of large phytoplankton, as other food, such as microzooplankton, may be important (Kleppel et al., 1991, 1998; Ohman and Runge, 1994; Runge and Plourde,

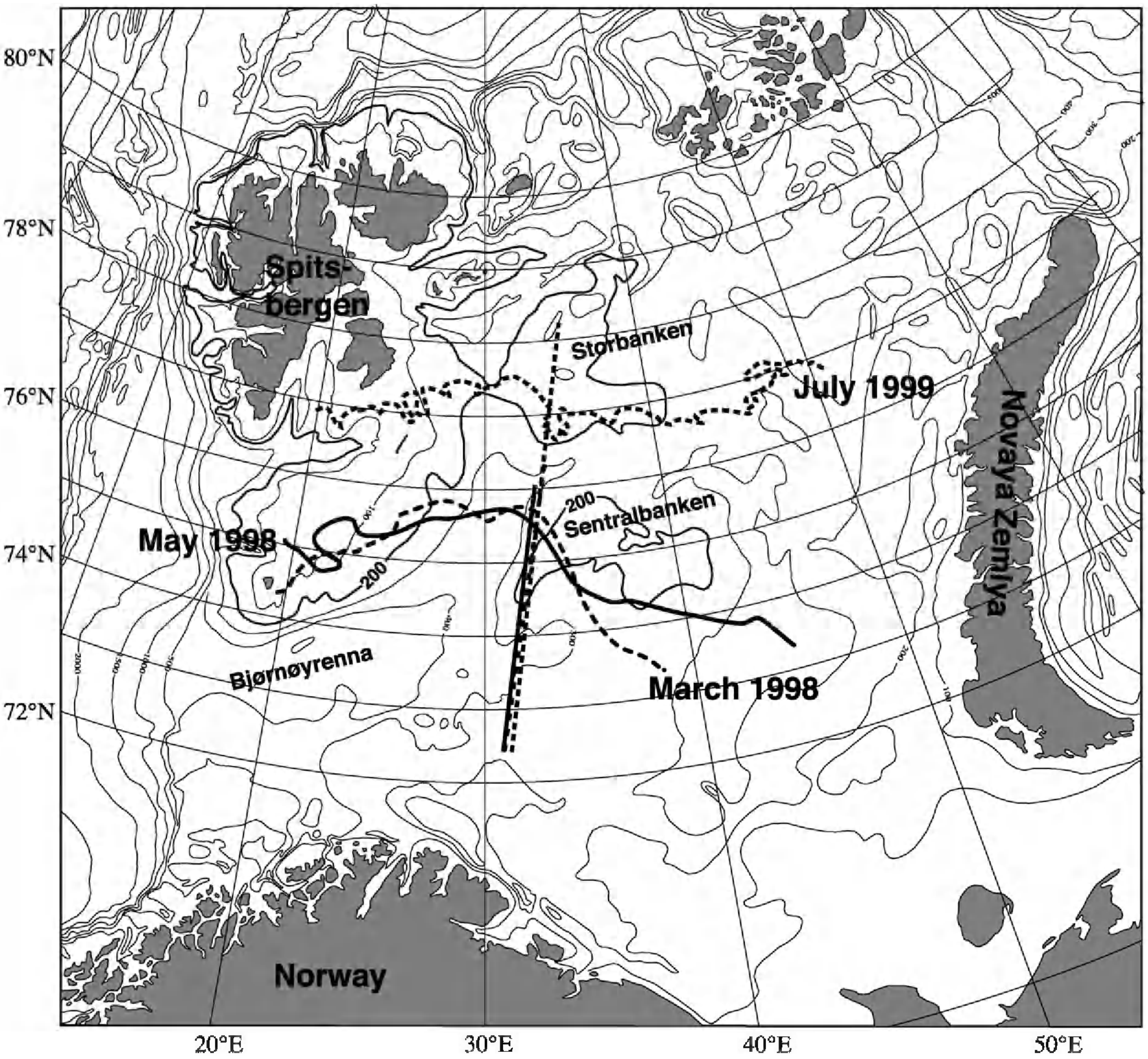

Fig. 1. Map of the study area of the Barents Sea. Three cruises, in March and May 1998 and July 1999, are indicated.

1996). Changes in the food environment might also have prolonged effects on subsequent reproduction (Båmstedt et al., 1999). Reproduction of copepods usually depends on both the previously accumulated energy reserves and current feeding success. However, the largest of the three species *C. hyperboreus* was shown to reproduce before the phytoplankton bloom, using only its lipids reserves for reproduction (Sømme, 1934; Østvedt, 1955; Conover, 1967; Smith, 1990; Hirche and Niehoff, 1996). The connection between reproduction activity and current feeding was many times shown in laboratory experiments, but is usually not so evident from the field data. A part of the discrepancy is reproduction dependence not only on current feeding, but also on lipid reserves, another—spatial and temporal variability of the environment. A temporal scale of research may also influence the result of comparison between reproduction and feeding activity, as there is always a lag between ingestion and egg production. Responses to changes in food concentrations, effects of season on egg production have to be studied thoroughly. The easiest, although indirect, way to estimate feeding activity of copepods in the field is to evaluate the subsequent products of their feeding, that is, faecal pellet matter egested by them. It was shown to be an appropriate index of feeding activity (Drits, 1985; Ayukai and Nishizawa, 1986; Tsuda and Nemoto, 1990; Rey et al., 1999; Frangoulis et al., 2001).

A major loss of phytoplankton-derived organic carbon from the euphotic zone occurs through zooplankton faecal pellets, detritus and settling of phytoplankton cells (Wassmann, 1989). The sinking of particulate organic matter supplies the inhabitants of the deeper layers and benthic communities with energy (Smetacek, 1984). The studied copepods produce relatively large faecal pellets with high sinking rates. As they are membrane covered, they do not disintegrate as quickly as others. This increases their role in the vertical pellet flux. Bearing in mind a significant role of *Calanus* spp. in zooplankton biomass in the Barents Sea (Skjoldal and Rey, 1989; Tande, 1991), a considerable impact of their faecal pellets on the vertical flux could be assumed.

The main objectives of this study were:

1. How was *Calanus* spp. feeding activity related to seasonal changes in food availability?
2. How did the proportion of *Calanus* spp. pellets in the vertical carbon flux change during the season?
3. How was *Calanus* egg production related to grazing on different temporal scales (monthly, daily, hourly)?

## 2. Materials and methods

Data were collected during three cruises of R/V "Jan Mayen" to the Barents Sea in March 1998, May 1998 and July 1999. Each cruise started with a transect running from Nordkapp at the south over the Central Bank to the Marginal Ice Zone (Fig. 1). On the way back, three to five 24-h stations were carried out (Table 1). Deployment of sediment traps, rate

Table 1
Dates and locations of the 24-h stations. Total depth and water bodies indicated

| Cruise | Station | Date | Location (°N °E) | Depth, m | Water body |
|---|---|---|---|---|---|
| I | 1 | 23 March 1998 | 72°55′ 30°98′ | 300 | Atlantic |
| | 2 | 21 March 1998 | 73°77′ 31°88′ | 350 | Polar Front |
| | 3 | 19 March 1998 | 76°39′ 33°21′ | 256 | MIZ |
| II | 1 | 28 May 1998 | 72°50′ 30°95′ | 301 | Atlantic |
| | 2 | 26 May 1998 | 73°79′ 31°64′ | 340 | Atlantic |
| | 3 | 24 May 1998 | 74°80′ 32°46′ | 168 | Polar Front |
| | 4 | 22 May 1998 | 75°61′ 33°06′ | 239 | Arctic |
| | 5 | 20 May 1998 | 76°02′ 32°99′ | 323 | Arctic |
| III | 1 | 9 July 1999 | 73°80′ 31°78′ | 342 | Atlantic |
| | 2 | 8 July 1999 | 75°12′ 32°29′ | 250 | Polar Front |
| | 3 | 6 July 1999 | 77°08′ 33°82′ | 169 | Arctic |
| | 4 | 4 July 1999 | 77°65′ 34°21′ | 190 | Arctic |
| | 5 | 2 July 1999 | 78°24′ 34°23′ | 194 | Arctic |

measurements, stratified zooplankton sampling were performed at these stations. The present study is based on the data from these stations. Water temperature changed at the 24-h stations from 2–3 to 3 °C and 4–5 °C in the Atlantic water in March, May and July in the upper 100 m layer, and was almost constantly around 1 °C in the Arctic water (Reigstad et al., 2002).

Sampling of the suspended matter with water bottles, sedimented matter with traps, and zooplankton with a plankton net has been in detail described elsewhere (Wexels Riser et al., 2002; Arashkevich et al., 2002). Samples of suspended matter were collected from 10, 30, 75 and 90 m in March 1998 and from 10, 30, 50, 100 and 150 m in May 1998 and July 1999. Samples were taken twice a day, at noon and midnight, with 10-l Niskin bottles. They were concentrated with a 20-μm sieve and preserved with glutaraldehyde (2% final concentration). Faecal pellets, eggs and nauplii from suspended samples were identified, counted and measured under a dissecting microscope in a plankton counting chamber. The length and width of the pellets were measured and the pellet volume calculated using appropriate stereometrical configurations (Edler, 1979). A volumetric carbon conversion factor of 69.4 μg C mm$^{-3}$ (Riebesell et al., 1995) was applied to estimate the faecal carbon.

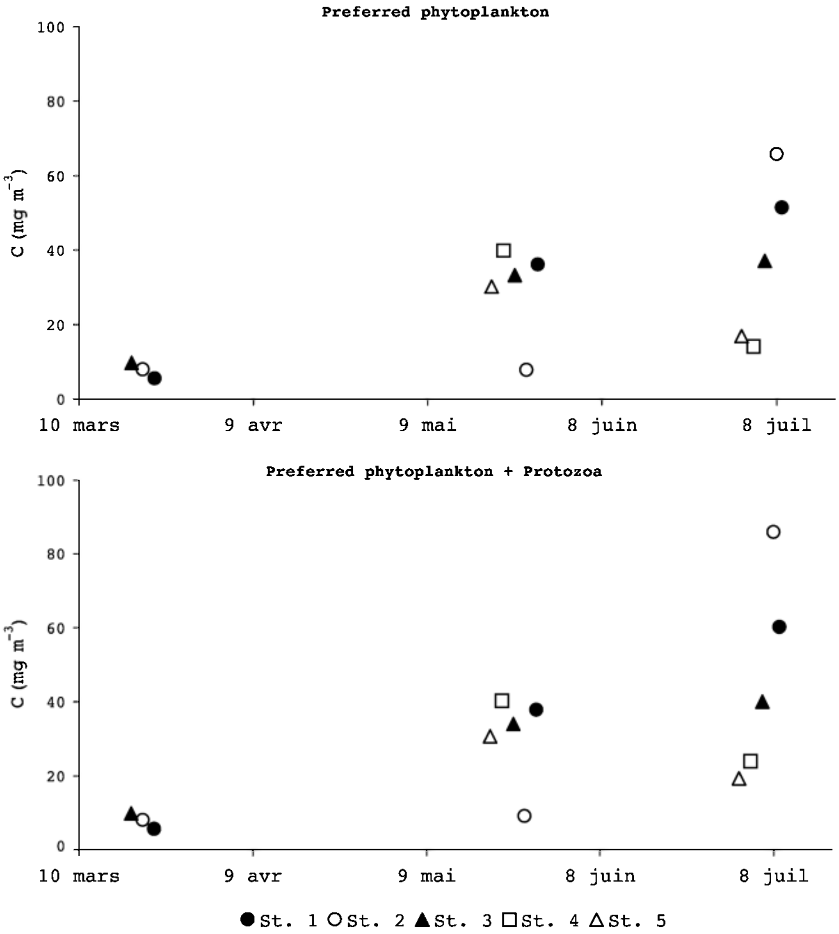

Fig. 2. Seasonal changes in concentration of the "preferred" food at the 24-h stations in the 0–90 m layer (see Materials and Methods for explanation of the composition of "preferred food"). Solid circles—Stn. 1, open circles—Stn. 2, solid triangles—Stn. 3, open squares—Stn. 4, open triangles—Stn. 5.

The whole samples of suspended matter were analyzed to assess the concentration of eggs, nauplii and faecal pellets of *Calanus* spp. Usually 30–300 specimens of each distinguished category of these items per sample were counted. However, due to a low abundance of suspended particles in March, these numbers were not more than 6–30. Total abundance of pellets, eggs and nauplii were estimated for the upper 0–100 m, in March cruise, 0–90 m layer. Mean daily values (an average for the noon and midnight values) were used. *Calanus* spp. faecal pellets carbon was used as an index of feeding activity (Drits, 1985; Ayukai and Nishizawa, 1986; Tsuda and Nemoto, 1990; Rey et al., 1999; and reference therein; Frangoulis et al., 2001). We distinguished *Calanus* spp. faecal pellets on the basis of their general appearance and dimensions (Gonzalez et al., 1994 and references therein; Pasternak et al., 2000). Faecal pellets of *Calanus* spp. have cylindrical shape, a well-developed peritrophic membrane, that forms usually one rounded and another elongated end. Four size classes of cylindrical pellets were distinguished. Average length and width and size range of the smallest pellets of this category was 100 × 20 and (50–100) × (10–20) μm, and they were assumed to be produced by small copepods; larger pellets of the mean length and width of 200 × 35 and size range (150–250) × (30 × 40) μm were produced by *Metridia* spp. and younger stages of *Calanus* spp. The two largest size classes, (250–550) × (50 × 70) and (550–1000) × (70 × 80) μm, belonged to the older copepodite stages of *Calanus* spp. *Metridia* spp. faecal pellets are wider and shorter, and usually more dense and dark than *Calanus* spp. However, to reduce the potential errors connected with separating their pellets, we took into consideration only the two largest size classes. There could be some further errors, if the pellets were broken and badly disrupted. However, there were not many of those during our cruises.

Sediment traps on a drifter were deployed at 30, 40, 50, 60, 90, 120, 150 and 200 m. The material was collected in Plexiglas cylinders of 450 mm length and with an aspect ratio of 6.2. The content of each trap (1.75 l) was collected after 24-h deployment and 100 ml subsamples for microscopic examination and counting of faecal pellets were preserved with glutaraldehyde (2% final concentration). The whole subsamples of 100 ml from sediment traps were analyzed. Usually 30–150 specimens of each distinguished category per sample were counted. However, due to a low abundance of sedimented particles in March, these numbers were not more than 5–20.

Mezozooplankton was collected with a WP-2 plankton net (0.5 m mouth diameter, 180 μm mesh).

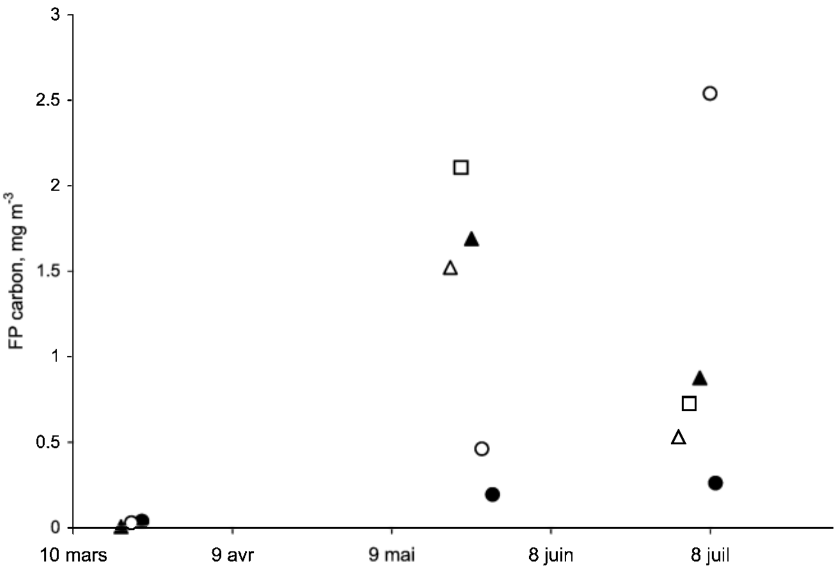

Fig. 3. Seasonal changes in total zooplankton faecal pellet carbon content in the upper 0–100 m layer at the 24-h stations. Symbols—as in Fig. 1.

Vertical tows from 0–50, 50–100, and 100–bottom layers were taken at the 24-h stations. The samples were preserved with a mixture of borax-buffered formaldehyde (4% final concentration) and propandiol solution (5% by volume). Identification and counting of zooplankton was carried out under a dissecting microscope.

The experiments on egg and faecal pellet production of the three copepod species were carried out during the May 1998 cruise. Ten (if available) freshly caught females of each of the three species (*C. finmarchicus*, *C. glacialis*, *C. hyperboreus*) at every 24-h station were sorted immediately for egg and faecal pellet production experiments. Females picked up at random were placed individually into a 200-ml glass dish with natural sea water in a temperature-controlled room at 1–3 °C. Experiments lasted for 3–5 days, but to determine clutch size and egg produc-

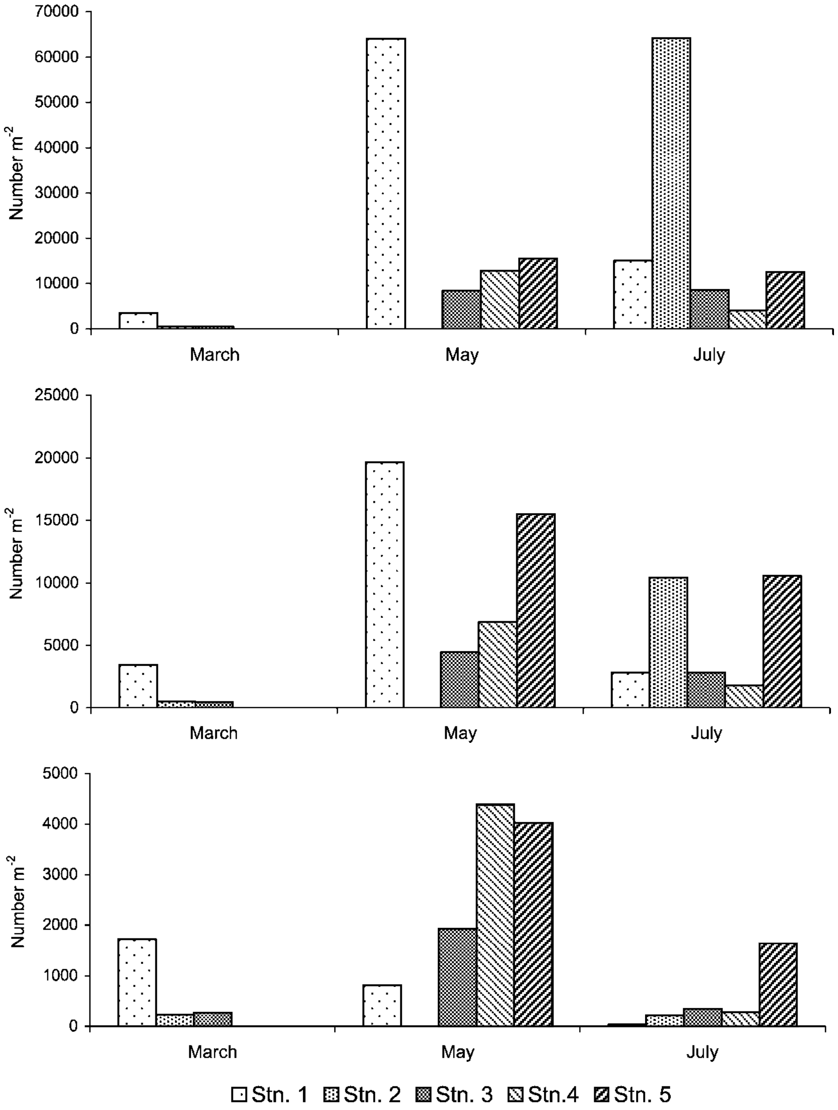

Fig. 4. Seasonal changes in abundance of *Calanus* spp. in the 0–100 m layer. Upper panel—abundance of all copepodite stages; median panel—abundance of older copepodite stages (CIV–CVI); lower panel—abundance of adult females.

tion per female per day, we used only data from the first 2 days, as clutch size decreased considerably after that in some replicates. To determine assumed dependence of egg production on feeding on daily basis, experimental dishes were checked twice a day, produced eggs and faecal pellets collected with a fine pipette, counted and removed, and water replaced. Means and standard errors for each experiment were calculated. To study relationship between egg production and feeding on an hourly basis, two experiments, where eggs and pellets from individual *C. finmarchicus* females were counted and removed every 2 h, were carried out at 24-h stations 4 and 5.

We compared concentration of *Calanus* spp. faecal pellets and eggs with the data on phytoplankton and Protozoa presented by Ratkova and Wassmann (2002). Phytoplankton species composition can strongly influence actual feeding conditions of copepods. *Calanus*' preference of diatoms and, sometimes, of dinoflagellates, was confirmed in some recent studies (Meyer-Harms et al., 1999; Irigoien et al., 2000), as well as avoidance of cyanobacteria, pelagophytes, and "green algae". There is no clear indication whether *Phaeocystis* sp. is a suitable source for *Calanus* feeding; recent studies showed that *Phaeocystis pouchetii* and cryptophytes were

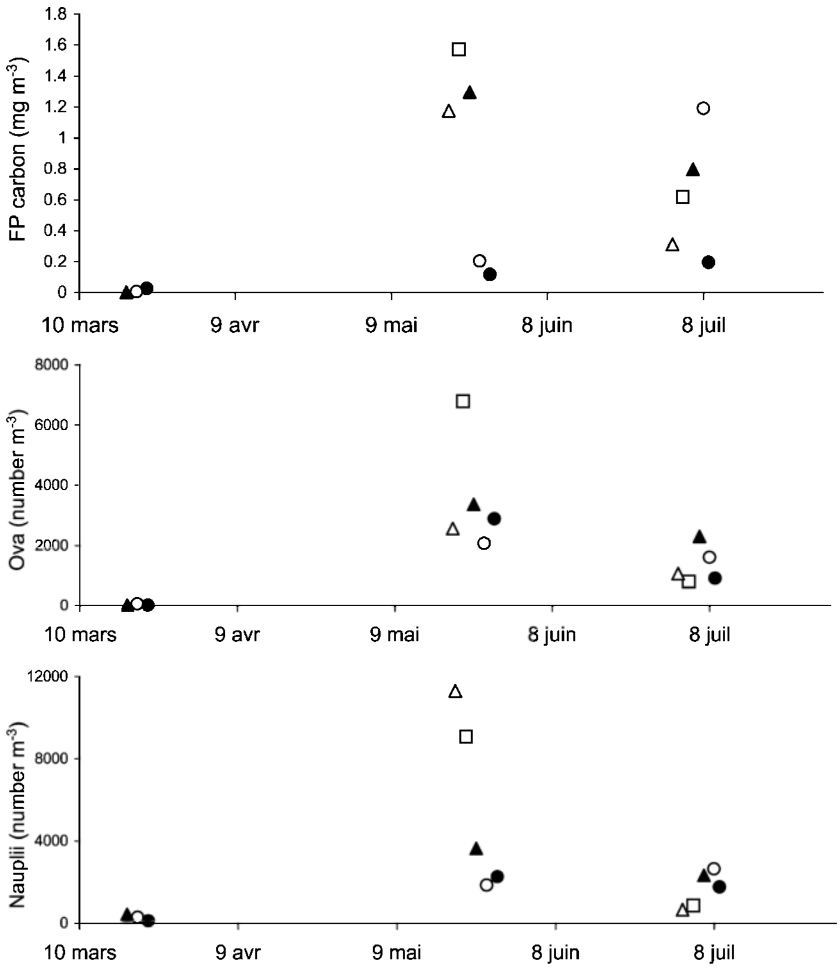

Fig. 5. Seasonal changes in feeding and reproduction output of *Calanus* spp. at the 24-h stations in the 0–100 m layer. Upper panel—concentration of faecal pellet carbon; median panel—concentration of suspended eggs; lower panel—concentration of nauplii. Symbols—as in Fig. 1.

ingested according to their abundance (Meyer-Harms et al., 1999). Some studies have demonstrated ingestion of *Phaeocystis* by calanoid copepods (Huntley et al., 1987; Tande and Båmstedt, 1987; Sargent and Falk-Petersen, 1988), others have inferred that it was not ingested (Bautista et al., 1992). As shown by Estep et al. (1990), predation upon *P. pouchetii* is a function of the physiological state of the colonies. For simplicity, we excluded *P. pouchetii* from the calculation of the assumed "preferred" phytoplankton food. Concentration of the "preferred" phytoplankton food, including diatoms, dinoflagellates, silicoflagellates, coccolithoforides (all >5 μm) was obtained for the 0–90 m layer. There is no indication whether silicoflagellates and coccolithoforides are selected by *Calanus* spp.; however, their biomass was much less than that of the first two groups (Ratkova and Wassmann, 2002), and we did not include them in the calculation of the "preferred" food.

Omnivory, especially feeding on protozoans, could play an important role for *C. finmarchicus*

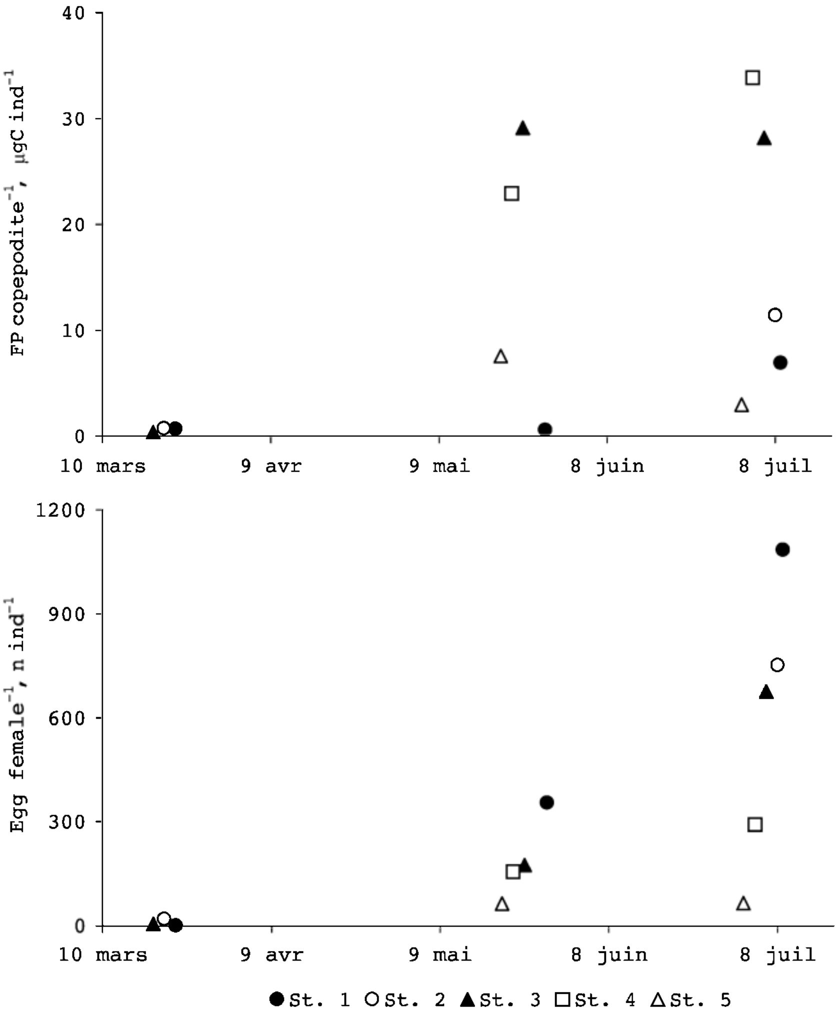

Fig. 6. Seasonal changes in specific indices of *Calanus* spp. feeding and reproduction activity. Upper panel—faecal pellet carbon per older copepodite of the three *Calanus* species; lower panel—number of eggs per female (*C. finmarchicus* and *C. glacialis*).

when phytoplankton resources are not abundant (Ohman and Runge, 1994). Thus, we made two calculations of the "preferred" food, with and without Protozoa (data from Ratkova and Wassmann, 2002). Spearman rank order correlations were calculated between total phytoplankton carbon, "preferred" food (with and without Protozoa), and suspended faecal pellets, ova and nauplii of *Calanus* spp. We also calculated specific values, that is, number of eggs per female and faecal pellet carbon per older copepodite.

## 3. Results

### 3.1. Seasonal changes in food availability

Chlorophyll concentration was low during the March cruise (0.01–0.04 mg $m^{-3}$ in the upper 40 m, Reigstad et al., (2002). Phytoplankton bloom was observed in May, with chlorophyll concentrations about 8–14 mg $m^{-3}$, which decreased in July (1–4.5 mg $m^{-3}$, Reigstad et al., 2002). Auto- and heterotrophic forms in the samples of the suspended pico-, nano- and microplankton were not distinguished and their combined biomass is later termed PNMC (pico-, nano- and microplankton carbon). There was no clear seasonal pattern in the changes of PNMC in the upper 0–90 m layer (Ratkova and Wassmann, 2002). Several groups such as *P. pouchetii*, probably heterotrophic flagellates, chrysomonades were responsible, forming occasional peaks at certain depths and stations (Ratkova and Wassmann, 2002).

The changes in the "preferred" food are shown in Fig. 2. The concentration of the "preferred" food was low in March; it increased in May and July. In July, the concentrations at the southernmost stations 1 and 2 were higher than those in May. No consistent pattern in concentration of the "preferred" food between stations was observed.

Protozoa were scarce in March and May (Ratkova and Wassmann, 2002) and their role in the "preferred" food biomass was negligible at that time (Fig. 2, upper and lower panels). Their abundance increased by July (Ratkova and Wassmann, 2002) and the pattern of their spatial distribution was the same as of the other "preferred" food.

### 3.2. Seasonal changes in concentration of faecal pellets

During the cruise in March, most of the zooplankton, and large copepods in particular, resided at the deep layers (Arashkevich et al., 2002). At that time, phytoplankton bloom had not yet started. Feeding activity of ascended zooplankton increased considerably during the bloom in May, which could be sup-

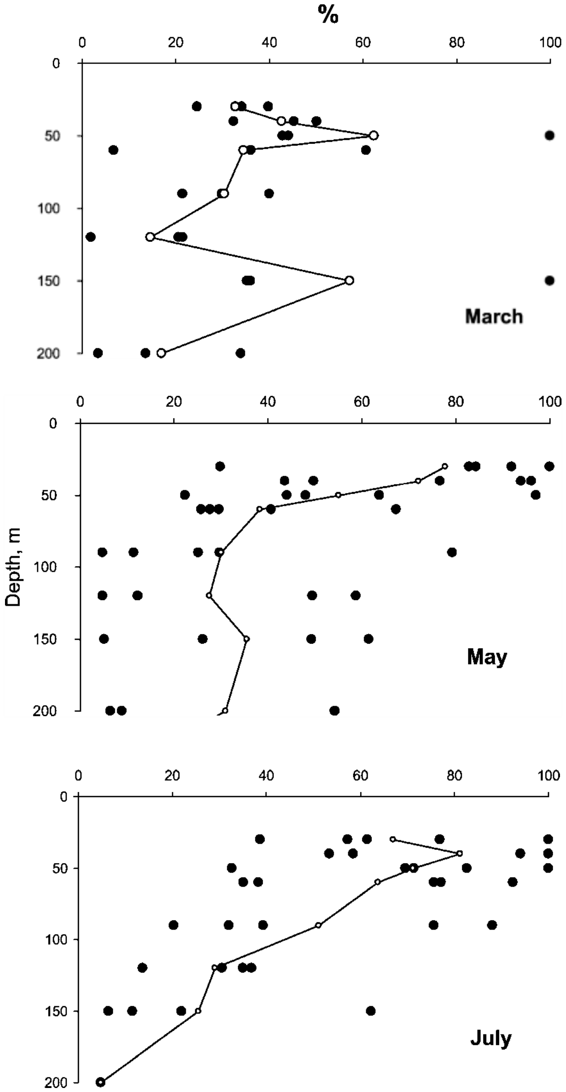

Fig. 7. Proportion of *Calanus* spp. faecal pellet carbon in total vertical flux. Data for 24-h stations are given. Means are along the lines.

Table 2
Spearman rank order correlations, $R_S$ ($p$), between concentration of phytoplankton carbon, preferred food carbon, *Calanus* spp. suspended faecal pellets, ova and nauplii, sampled during March, May and July cruises

| | Total phytopl. | Preferred food: phytopl. | Preferred food: phytopl.+ Protoz. | Faecal pellets | Ova | Nauplii |
|---|---|---|---|---|---|---|
| Total phytopl. | 1 | 0.36 *(0.223)* | 0.41 *(0.170)* | 0.16 *(0.590)* | 0.36 *( 0.223)* | 0.32 *(0.288)* |
| Preferred food: phytopl. | | 1 | 0.99 ***(0.0000)*** | 0.63 ***(0.020)*** | 0.59 ***(0.032)*** | 0.66 ***(0.014)*** |
| Preferred food: phytopl.+Protoz. | | | 1 | 0.66 ***(0.001)*** | 0.62 ***(0.025)*** | 0.69 ***(0.009)*** |
| Faecal pellets | | | | 1 | 0.68 ***(0.011)*** | 0.83 ***(0.0004)*** |
| Ova | | | | | 1 | 0.91 ***(0.0000)*** |
| Nauplii | | | | | | 1 |

posed from an increased concentration of faecal pellet carbon (Fig. 3). Abundance of different copepodite stages of *Calanus* spp. in the upper 100 m layer was very low in March and increased in May, remaining at a similar level in July (Fig. 4, upper panel). However, the age structure was different in May and July, and older copepodite stages (CIV–CVI, the producers of pellets we estimated) and, especially, adult females were more numerous in May (Fig. 4, median and lower panel). Feeding activity of *Calanus* spp. in March as evaluated from faecal pellets in the samples of suspended matter (Fig. 5, upper panel) and from the visual estimates of gut fullness was very low. On average, 8 ± 9.6% (mean ± S.D.) of the *Calanus* spp. older stages at different 24-h stations in March contained food inside. The ratio of *Calanus* faecal pellets to older copepodites also was low in March (less than 1 μg C ind$^{-1}$, Fig. 6, upper panel). During the bloom in May, about 85% of *Calanus* spp. contained food in the guts. The ratio of *Calanus* faecal pellets to older copepodites increased considerably (up to 29 μg C ind$^{-1}$, Fig. 6, upper panel). The highest concentration of total suspended zooplankton faecal pellets in the upper 0–100 m layer was found at the 24-h stations 5 and 4 (close to the ice). Pellet concentration decreased southward. In July, concentration of *Calanus* faecal pellets was generally lower, with the exception of Stn. 2, where a pronounced increase was noted. However, the specific values for the older copepodites were similar to those in May (Fig. 6, upper panel).

*Calanus* pellets changed similarly to the total faecal pellet carbon (Figs. 3 and 5, upper panel). The peak of *Calanus* spp. faecal pellets at Stn. 2 in July was not so pronounced as in total faecal carbon; otherwise, there was a remarkable coincidence. Indeed, the average proportion of *Calanus* spp. pellets suspended in the upper water layer was fairly stable and high throughout the study period, varying from 48% to 95% of total FP carbon. Thus, *Calanus* spp. egestion accounted, usually, for a major portion of the suspended total FP concentration (of the size >than 50 μm) in the 0–100 m water layer. *Calanus* faecal pellets usually comprised also more than 50%, on average, of sediment faecal material in the upper water layer, and their role decreased only in deeper layers (Fig. 7). However, the March data should be treated with caution, as both the *Calanus* spp. FP and the total zooplankton FP abundance were low. Filiform pellets from krill, whose role increased at the deep layers, dominated the sediment traps at Stns. 1 and 4 in May and were also important in July, being the second main contributor to the vertical pellet flux (Wexels Riser et al., 2002).

There was no correlation between *Calanus* faecal pellet and total phytoplankton carbon, but a weak but significant correlation with "preferred" phytoplankton was found (Table 2). Addition of heterotrophic

Table 3
Spearman rank order correlations, $R_S$ ($p$), between phytoplankton carbon, preferred food carbon, specific values of *Calanus* spp. faecal pellets (micrograms per older copepodite) and ova (number per female), sampled during March, May and July cruises

| Food | Faecal pellets | Ova |
|---|---|---|
| Total phytoplankton | − 0.01<br>*(0.966)* | 0.34<br>*(0.276)* |
| Preferred food: phytoplankton | 0.40<br>*(0.199)* | 0.85<br>***(0.0004)*** |
| Preferred food: phytoplankton + Protozoa | 0.45<br>*(0.088)* | 0.87<br>***(0.0002)*** |

microplankton carbon to the preferred food slightly strengthened the correlation (Table 2). The correlations between the individual specific values (faecal pellet carbon per older copepodite) and the food resources were not significant (Table 3).

### *3.3. Seasonal variations in abundance of eggs and nauplii*

Reproduction had just started during the March cruise; concentration of eggs and nauplii of *Calanus*

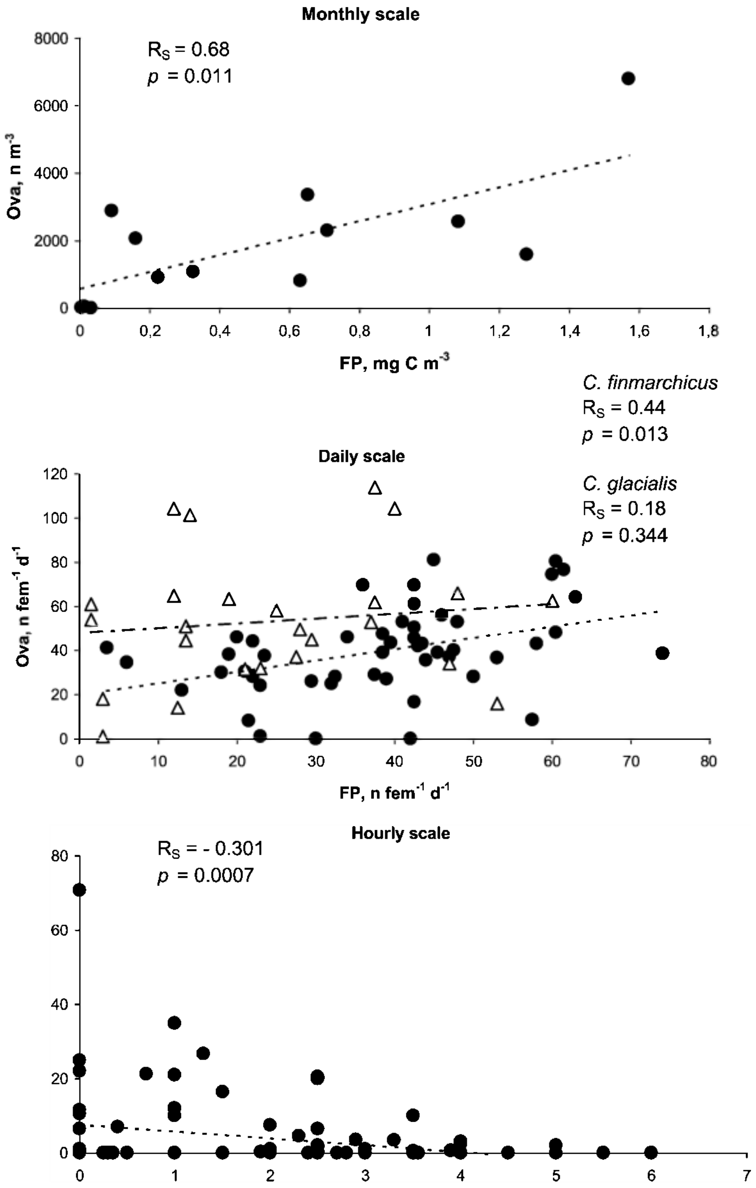

Fig. 8. Relationship between feeding activity and egg production of *Calanus* spp. Upper panel—concentration of suspended eggs vs. faecal pellets, field data. Median panel—number of eggs vs. number of faecal pellets produced daily by a female in the experiment. Dark circles: *C. finmarchicus*, open triangles: *C. glacialis*. Lower panel—number of eggs vs. number of faecal pellets produced hourly by a female *C. finmarchicus*. Spearman rank order correlation coefficients ($R_S$) and $p$-levels are given. Trend lines are shown.

spp. was low (Fig. 5, median and lower panels). Both *C. glacialis* and *C. finmarchicus* were actively reproducing in May. About 90% females were at gonad stage 4, that is, fully mature, and were filled with eggs. *C. hyperboreus* females, on the contrary, were unripe (gonad stage 1) and did not contain eggs. Concentration of eggs and nauplii in the ambient water considerably increased, peaking at the northernmost Stn. 5 (ice station) and gradually decreasing southward (Fig. 5, median and lower panels). Although the reproduction of the two *Calanus* species continued in July, the concentration of eggs and nauplii dropped down at almost all of the 24-h stations, except Stn. 2, where they exceeded the May values. However, the number of eggs per female consistently increased from March to July (Fig. 6, lower panel). Anyway, the peak of reproduction was observed in May, as the number of reproducing adult females was then the highest (Fig. 5, lower panel).

In our field data, abundance of *Calanus* ova and nauplii closely followed the same seasonal trend as the concentration of FP, which was regarded as an index of feeding activity (Fig. 5, upper panel). In an attempt to understand how reproductive and feeding activities in *Calanus* were connected, we plotted ova versus faecal pellet concentration. Correlation between suspended *Calanus* ova and FP from different cruises is significant (Fig. 8, upper panel; Table 2).

### *3.4. Production of eggs and faecal pellets in experiments*

In experiments, *C. finmarchicus* females produced, on average, from 28 to 53 eggs day$^{-1}$, and *C. glacialis*—from 16 to 66 eggs day$^{-1}$ in different experiments (Table 4). This difference was significant (Kruskal–Wallis test, $H = 5.229$, $p = 0.022$). Maximum number of eggs was produced by *C. finmarchicus* at Stn. 3 (150 eggs fem$^{-1}$ day$^{-1}$ at day 3) and by *C. glacialis* at Stn. 5 (130 eggs fem$^{-1}$ day$^{-1}$ at day 3). *C. hyperboreus* never produced eggs during the experiments in May, all females possessed undeveloped gonads. Mean production of faecal pellets by *C. finmarchicus* varied from 25 to 51 FP ind$^{-1}$, *C. glacialis* 15 to 40, *C. hyperboreus* 14 to 48 (FP production of *C. finmarchicus* and *C. glacialis* differed significantly: Kruskal–Wallis test, $H = 7.85$, $p = 0.005$; FP production of *C. glacialis* and *C. hyperboreus* did not: $H = 2.27$, $p = 0.322$). A slight significant positive connection was found between mean daily production of eggs and egested faecal pellets of *C. finmarchicus* (Spearman rank order correlation: $R_S = 0.44$, $p = 0.013$) and slight insignificant *C. glacialis* (Spearman rank order correlation: $R_S = 0.18$, $p = 0.344$) (Fig. 8, median panel).

Table 4
*Calanus* spp. egg and faecal pellet daily production in experiments. Means ± standard errors (S.E.) and number of replicates are given

| Station | Species | *N*, replicate | Eggs | | Faecal pellets | |
|---|---|---|---|---|---|---|
| | | | Mean | S.E. | Mean | S.E. |
| 1 | *C. finmarchicus* | 9 | 35.7 | 3.35 | 24.8 | 3.37 |
| | *C. glacialis* | 2 | 16.5 | 21.90 | 13 | 14.10 |
| 2 | *C. finmarchicus* | 7 | 28.3 | 4.09 | 31.8 | 3.84 |
| | *C. glacialis* | 3 | 49.2 | 11.89 | 15.5 | 3.41 |
| 3 | *C. finmarchicus* | 10 | 53.0 | 7.72 | 42.4 | 5.29 |
| | *C. glacialis* | 12 | 52.5 | 9.40 | 24.4 | 5.79 |
| | *C. hyperboreus* | 5 | 0 | 0 | 38 | 7.54 |
| 4 | *C. finmarchicus* | 10 | 32.0 | 8.57 | 34.2 | 4.93 |
| | *C. glacialis* | 3 | 53.7 | 6.73 | 23.2 | 8.69 |
| | *C. hyperboreus* | 7 | 0 | 0 | 14 | 5.36 |
| 5 | *C. finmarchicus* | 14 | 43.9 | 4.24 | 51 | 3.03 |
| | *C. glacialis* | 8 | 66.6 | 10.14 | 39.6 | 4.56 |
| | *C. hyperboreus* | 6 | 0 | 0 | 48.5 | 8.15 |

In the experiments, when produced eggs were counted every second hour, we noted that during egg release, females usually stopped feeding and egesting pellets. A slight, but significant negative correlation was found between egg and faecal pellet production on the short-term (hourly) basis (Fig. 8, lower panel). Thus, the correlations between *Calanus* egg production and feeding activity changed depending on the scale of analysis from positive significant (monthly scale) through positive significant with a lower coefficient of correlation (*C. finmarchicus*), or, positive insignificant (*C. glacialis*) (daily scale) to negative significant (hourly scale) (Fig. 8).

## 4. Discussion

Low abundance of *Calanus* spp. faecal pellets in March reflects the fact that most of these copepods still inhabited the overwintering depth layers (Arashkevich et al., 2002). Moreover, feeding activity of those ascended to the upper layer in spite of a high

PNM carbon (from 51 to 388 mg $m^{-3}$ versus 101–301 in May and 125–216 in July, Ratkova and Wassmann, 2002) was not high. It seems *Calanus*' populations were yet in the state of transition from winter to spring. Another aspect is that the high concentration of PNMC was formed mainly by chrysophytes, *P. pouchetii*, flagellates, and picophytoplankton, which do not belong to the group of "preferred" food items.

At the majority of the 24-h stations, the concentration of *Calanus* spp. faecal pellets was the highest in May. This reflects the abundance of *Calanus* populations and their feeding activity. After an increase of the abundance in the upper layer in May, *Calanus* spp. population remained rather similar in numbers with the exceptions of Stn. 1 in May and Stn. 2 in July (Fig. 4; Arashkevich et al., 2002), where *Calanus* was about three times more abundant. However, if the difference in *Calanus* abundance between stations in July was reflected in the FP data (both *Calanus* and their faecal pellets were extremely abundant at Stn. 2), it was not in the May data (Figs. 4 and 5, upper panel). Neither the abundance of *Calanus* (Fig. 4), nor the concentration of the preferred food, which was high (Fig. 2), can explain the low FP concentration at Stn. 1 in May. Consequently, the specific value (faecal pellet carbon per older copepodite) was extremely low at Stn. 1 in May (Fig. 6, upper panel). Perhaps, this could be connected with the high proportion of *P. pouchetii*, as at both stations (Stn. 2 with high and Stn. 1 with low "preferred" phytoplankton carbon), where faecal pellet concentration was low, *Phaeocystis* impact on the total phytoplankton carbon exceeded that of the preferred phytoplankton by a factor of 5 and 7. *P. pouchetii* produced plenty of mucous matter, which could cause a decrease in feeding activity. The results of the recent paper by Frangoulis et al. (2001) supported the idea of lower feeding of copepods under *Phaeocystis* sp. bloom conditions. Faecal pellet distribution in July coincided with the "preferred" food concentration.

Among the variables which influence feeding and assimilation/pellet production in copepods, food quality is certainly the most difficult to describe. In the recent review on the biology of calanoid copepods, Mauchline (1998) wrote: "The percentage weight of ingested food that is assimilated varies greatly. Assimilation efficiencies vary (primarily) with the ash content of the food...Assimilation efficiency of 60 to 70% is usually assumed for herbivorous species". In the classic paper by Marshall and Orr (1955), assimilation of the four diatom species by *C. finmarchicus* was tested, the average being always over 50%. Mean assimilation varied from 47% to 98% between five tested dinoflagellates species. Thus, assimilation efficiency varied approximately by a factor of 2 between different species within diatoms and dinoflagellates similarly. Flagellates were utilized usually at a lower rate. Mayzaud et al. (1998) indicated that "Assimilation is...a function of nutrient content in food, gut fullness, digestibility, availability of organic compounds, digestive enzyme activity and assimilation capability of the copepod". Recently, the relationship between the rates of ingestion and defecation and assimilation efficiency of the omnivorous copepod *Aractia tonsa* was examined experimentally with different diets (Besiktepe and Dam, 2002). However, the experiments carried out on the herbivorous species *C. glacialis*, which was also studied in the present paper, showed that the number of faecal pellets produced daily by copepods fed with different species of diatoms, dinoflagellates, and detritus at superabundant concentrations, was almost equal (90 ± 11 pellets $ind^{-1}$ $day^{-1}$) (Arashkevich and Sergeeva, 1991). This allowed the authors to suggest that changes in assimilation efficiency could influence primarily not the number of egested pellets, but density of packing of evacuated matter. An assessment of seasonal changes in assimilation efficiency (or, pellet production per unit of ingested food) connected with the change of the diet because of a different phytoplankton composition is a goal for a special and serious research.

Diets of calanoid copepods feeding in the sea were not unialgal; they included different groups and species (our unpublished data on gut content analysis). In the sea, diatoms made up from 3.5% to 24.5% of the total phytoplankton at different stations in May and from 0.5% to 19.8% in July. So, on the one hand, assimilation efficiency, which determines the relationship between feeding activity and pellet production, is highly variable, and we have no ground to apply different values during the season. On the other hand, although mean proportion of diatoms decreased in

July compared with May, this decrease was not a dramatic one, and could not play a considerable role in the approach used here.

While no correlation was found between faecal pellet and total phytoplankton carbon, a weak but significant correlation with “preferred” phytoplankton was (Table 2). As the proportion of Protozoa in microplankton biomass was not high (Ratkova and Wassmann, 2002), addition of this group to the preferred food only slightly changed the correlation making it more close (Table 2). However, the correlations between the individual specific values (faecal pellet carbon per older copepodite) and the food resources were not significant (Table 3). Perhaps, the main reason for this discrepancy was that in spite of the highest food concentration at Stns. 1 and 2 in July, many of the *C. finmarchicus* older copepodites were not feeding in July. At that time, they stopped feeding and commenced the descent to the overwintering depths (Arashkevich et al., 2002). As we have no data on the proportion of feeding copepods in July, we had to use the total concentration of older *Calanus* copepodites, which could cause an underestimation. Another factor could be further reduction of the number of not numerous cases for statistical analyses (there are no data on zooplankton at Stn. 2 in May).

The proportion of eggs per *Calanus* female, on the other hand, is closely correlated with the potential food (Table 3). Under other circumstances (females feeding during the spring phytoplankton bloom), egg production in *C. finmarchicus* in the Norwegian Sea was clearly related not only to the phytoplankton ingestion but also to the total phytoplankton concentration (>5 μm) (Irigoien et al., 1998).

The observed decrease in the total number of suspended eggs in July was clearly connected with a pronounced decrease in abundance of females (Fig. 4, lower panel). The number of eggs per female was even higher than in May (Fig. 6, lower panel). A reduced hatching time due to increased temperature could be suggested in July. However, water temperature was almost the same in the Arctic water during all three cruises (around 1 °C), and changed only in the Atlantic water: from 2–3 °C to 3 °C and 4–5 °C in March, May and July, accordingly, in the upper 100 m layer (Reigstad et al., 2002). This difference is too small to influence noticeably the sort of estimation we carried out in this study, taking into account the dependence of hatching time on temperature (Corkett et al., 1986; McLaren et al., 1988), as well as the fact that only one of the 24-h stations was performed in the Atlantic water in July, when the temperature increase occurred.

The ingestion and reproduction of copepods are basically closely coupled. Gonad formation and maturation were shown to be fuelled by internal energy reserves (previous feeding success), but major egg-laying activities were suggested to rely on external sources (e.g., Tande, 1982; Plourde and Runge, 1993; Hagen and Schnack-Schiel, 1996; Hirche, 1996b). Thus, egg production should be the result of interactions of the two factors: (a) previous lipid storage and (b) presently available food, or actual ingestion, which explains the relation between ingestion and egg production rate frequently observed (Marshall and Orr, 1952; Runge, 1985; Hirche, 1990, 1996b; Hirche et al., 1991, 1997; Niehoff et al., 1999). In the present study, abundance of *Calanus* ova and nauplii were closely and significantly correlated with the concentration of their faecal pellets, that is, their feeding activity (Fig. 5, Table 2). The individual specific value (concentration of *Calanus* eggs to adult females) is even more closely correlated with the potential food (Table 3). This points to the important role of the actual ingestion versus stored lipid reserves in supplying reproduction with energy in the studied area of the Barents Sea.

*C. glacialis* and *C. finmarchicus* were actively reproducing during the phytoplankton bloom in May. April–May was reported to be the spawning period of *C. finmarchicus* in the Barents Sea (review in Hirche, 1996b). Both *C. glacialis* and *C. finmarchicus* were indicated to start spawning in mid-April at the polar front of the Barents Sea (Tande, 1991). Other authors (Hansen et al., 1996) found that egg production of *C. glacialis* was practically ended for a year from the data of the cruise conducted to the same region in May 1993. The coupling of *Calanus* reproduction with phytoplankton bloom was monitored in various regions (Marshall and Orr, 1955; Diel and Tande, 1992; Gaard, 1996; Gislason and Astthorsson, 1996; Niehoff et al., 1999; Niehoff and Hirche, 2000). Mean and maximum individual daily egg production rates obtained in our experiments are close to the highest rates usually reported (Marshall and Orr, 1952; Hirche, 1989; Diel and Tande, 1992; Kosobokova, 1993;

Plourde and Runge, 1993; Hansen et al., 1996; Hirche et al., 1997; Niehoff et al., 1999). *C. hyperboreus* did not produce eggs; all females possessed undeveloped gonads. This is no surprise, as this species is known to reproduce earlier, well in advance of the spring bloom (Sømme, 1934; Østvedt, 1955; Conover, 1967; Smith, 1990; Hirche and Niehoff, 1996).

The general relationship between mean daily production of eggs and ingestion could be masked by various influences. The often observed lack of correlation between mean daily production of eggs and egested faecal pellets could be explained by a delay response in egg production to feeding conditions which indicates the existence of a buffer of nutrients (Hirche, 1990; Hirche et al., 1997). Patchiness in distribution of both food and copepods as well as a feeding history of reproducing females could also influence the relationship between individual egg and faecal pellet production rate. The results of mesocosm experiments showed that the effect of feeding history on ingestion rate could last up to 15 days (Rey et al., 1999). In these experiments, females of *C. finmarchicus* produced the same number of eggs after being transferred from different feeding conditions to superabundant food. However, females transferred from the low-food conditions produced significantly more faecal pellets. The authors concluded that both age and feeding history might be as important as other environmental factors such as temperature or food supply in explaining the variability in fecundity and egestion (Rey et al., 1999). In our experiments, a significant correlation was found for *C. finmarchicus*, and insignificant for *C. glacialis*. This may be caused by several reasons: fewer females of the latter species were analyzed (28 versus 50 of *C. finmarchicus*); the buffer of nutrients could be of more importance in *C. glacialis*, than in *C. finmarchicus*. One more possibility is that the egg production season of *C. glacialis* was, as it was mentioned above, close to the end (Hansen et al., 1996), and the population might contain a high proportion of ageing females which decrease the egg production rate (Diel and Tande, 1992; Plourde and Runge, 1993; Hirche 1996b).

A slight but significant negative correlation found between egg and faecal pellet production on the short-term (hourly) basis confirms that during spawning events, female feeding ceased. Perhaps, the coefficient of correlation would be higher if eggs and pellet production could be estimated more often (e.g., in half-an-hour intervals). Anyway, the correlations between *Calanus* egg production and feeding activity changed depending on the scale of analysis from positive significant (monthly scale) through positive significant with lower coefficient of correlation (*C. finmarchicus*), or positive insignificant (*C. glacialis*) (daily scale) to negative significant (hourly scale). Thus, relationship between reproduction and feeding of *Calanus* spp. could be different depending on a temporal scale.

Egg production rate of *Calanus* spp. depends on the season (Hirche et al., 1997), phase of spawning activity (Diel and Tande, 1992; Hirche, 1996b; Rey et al., 1999), temperature (Runge, 1984, 1985; Hirche, 1996b; Hirche et al., 1997), food quality (Marshall and Orr, 1952; Kleppel, 1993). Anyway, a considerable part of variability (68%) in our study was connected with feeding activity.

## 5. Conclusion

The results of this study confirmed the importance of *Calanus* spp. as major contributors to the suspended matter and vertical flux in the marginal ice zone and the open Barents Sea in March–July. Proportion of *Calanus* spp. faecal pellets in suspended matter and in the total flux in the upper 100 m layer was high and rather stable throughout the study period. Feeding of calanoid copepods was correlated with the seasonal changes in their preferred food. Basically dependent on feeding success, egg production could be differently correlated with feeding activity depending on the temporal scales of the study (monthly, daily, hourly). Significant correlations between indices of current feeding activity (or, available food) and egg production and nauplii concentration obtained in the field suggest that current feeding played a major role in supplying of reproduction with energy, compared to the lipid reserves.

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