

A high frequency time series at weathership M, Norwegian Sea, during the 1997 spring bloom: feeding of adult female *Calanus finmarchicus*

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ABSTRACT: The feeding ecology of *Calanus finmarchicus* was investigated during spring 1997 at a permanent station in the Norwegian Sea (Stn M, 66°N, 2°E) as part of the TASC (Trans Atlantic Study of *Calanus finmarchicus*) project time-series investigations. The phytoplankton bloom began in mid May, coinciding with the onset of the stratification, and was mainly composed of diatoms and prymnesiophytes. Daily ingestion of phytoplankton by *C. finmarchicus* was about 2% of body carbon for the long period before the bloom, 30% during the bloom and 14% after the bloom. Due to their low abundance, ingestion of ciliates represented only 2 to 6% of the phytoplankton ingestion. Body carbon and carbon/nitrogen ratio decreased significantly before the bloom indicating a deficit in carbon ingestion and the use of storage lipid during this period.

KEY WORDS: *Calanus finmarchicus* · Norwegian Sea · Feeding · Phytoplankton · Ciliates

INTRODUCTION

Calanus finmarchicus is a dominant component of North Atlantic zooplankton and is the main food of larvae of commercially important fish such as cod, haddock, capelin, herring and red-fish (Bainbridge & McKay 1968, Ellertsen et al. 1981, Kane 1984, Astorsson & Gislason 1997). *C. finmarchicus* is likely to play an important role in the recruitment success of these species (Burd 1963, Cushing 1982, Maravelias & Reid 1997). It has been suggested that interannual variability in climate could affect fish recruitment through links between the physical conditions, primary production and secondary production (see review in Runge 1988). Runge (1988) proposed that because of the higher sensitivity of the productivity of *C. finmarchicus* to food concentration, this species was most likely to form a strong link in the food chain from

phytoplankton to fish via copepods. This would be the case in the *Calanus* sp. dominated areas and *Calanus* feeding fish populations rather than in systems dominated by small copepods, which are less sensitive to changes in food concentration. Since the first work by Marshall (1924), feeding of the genus *Calanus* has been the subject of a large number of studies (see review in Harris 1996). Nevertheless, and because of obvious practical and infrastructure limitations, studies on variations of *C. finmarchicus* feeding rates in the open sea are scarce. Mechanisms controlling *C. finmarchicus* arousal are still not well understood (see review in Miller et al. 1991), but due to the strong influence of climatic conditions on the development of phytoplankton in the oceanic areas of the North Atlantic (Sverdrup 1953), the lapse of time between *C. finmarchicus* arousal and phytoplankton bloom can differ, not only between coast and open sea areas (Niehoff & Hirche 1997) but also between different areas in the open sea. As an example, south of Iceland (Stn India, 59°N, 18°W) arousal seems to coincide with

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the phytoplankton bloom with *C. finmarchicus* coming to the surface in mid April (Williams & Wallace 1975).

In contrast, in the Norwegian Sea (Stn M, 66°N, 2°E), *Calanus finmarchicus* arrives at the surface at the same time or even earlier than it does south of Iceland (Østvedt 1955, Lie 1968, Wiborg 1978), whereas the phytoplankton bloom does not occur until mid May (Halldal 1953, Dale 1995).

The objective of this work was to study feeding of *Calanus finmarchicus* in the open sea, from the arousal of the population until the development and decline of the spring phytoplankton bloom, focusing on the influence of environmental conditions, feeding activity before the bloom, the increase in feeding during the bloom, and the contribution of non-phytoplanktonic carbon sources and the effect of those factors on the carbon content of the animal.

MATERIALS AND METHODS

Stn M (Mike), 66°N and 2°E (Fig. 1), has been employed as a permanent weather station since 1948. The weather ship remains in an area of about 2.5 miles radius around this position for 28 d before taking 3 d to make a port call to change crew and re-supply. The depth is about 2000 m, but due to the slope, important variations in depth can be found in the drifting area (1500 to 3000 m). The station is situated on the western edge of the Norwegian Atlantic current, close to the frontal area with Arctic waters transported by the Iceland East current (Mosby 1950).

Samples were taken from 22 March to 9 June 1997. Measurements made on a daily basis were CTD profiles, total chlorophyll *a* concentration (chl *a*), gut fluorescence and, with some exceptions, individual carbon and nitrogen content of *Calanus finmarchicus*. Sam-

ples for fractionated chl *a* (>5 µm), pigment profiles by HPLC (methods of Barlow et al. 1997), total particulate carbon (TPC) and total particulate nitrogen (TPN) were taken once a week at 5, 10, 20, 30, 40, 50 and 60 m. Additionally several incubation experiments were performed to estimate feeding rates on ciliates.

Daily CTD (Seabird SB19) profiles were performed to 200 m, except on the days when HPLC and TPC vertical distribution samples were taken, then the profile was to 1200 m. Samples for chl *a* were taken with a rosette at 5, 10, 20, 30, 40, 50, 60, 80 and 100 m, filtered onto a Whatman GF/F filter (total chl *a*) or Nuclepore membrane filter (>5 µm chl *a*) and measured by fluorescence after 24 h extraction in 90 % acetone (Parsons et al. 1984). WP2 nets (500 µm) from 100 m to the surface were taken to collect animals for gut fluorescence at 09:00 and 21:00 h (22:00 h in the May-June period). Samples for gut fluorescence were immediately frozen in liquid nitrogen. Between 3 and 5 replicates of 10 adult female *Calanus finmarchicus* were sorted under a stereomicroscope, placed in 7 ml of 90 % acetone and the gut fluorescence measured after 24 h extraction. Estimates of body carbon and nitrogen were made on replicates of 10 *C. finmarchicus* from the same samples. Prosome lengths of adult females were measured and the specimens were dried at 50°C and then analyzed in a Carlo Erba CN analyzer.

Phytoplankton ingestion was estimated from gut fluorescence following the method of Mackas & Bohrer (1976): $I = Gf \times GCRC$, where *I* is ingestion, *Gf* is the gut fluorescence and GCRC is the gut clearance rate which was estimated from the temperature (Dam & Peterson 1988). No correction was made for possible pigment destruction. Filtration rates on phytoplankton were estimated by dividing the ingestion by the chl *a* concentration: $F = I/\text{chl } a$. In order to maintain a conservative approach to estimating *F* we used the maxi-

mum chl *a* concentration in the mixed layer. The C:chl *a* ratio was calculated following Banse (1977) from the slope of the TPC-chl *a* regression. Therefore chl *a* was converted into carbon using a C:chl *a* ratio of 62.

The marker pigments measured were chlorophyll *b*, alloxanthin, 19-hexanoyloxyfucoxanthin, fucoxanthin, 19-butanyloxyfucoxanthin and peridinin. The contribution of the different phytoplankton groups to chl *a* was estimated using CHEMTAX (Mackey et al. 1996).

During the study period the majority of the *Calanus finmarchicus* population remained in the upper 50 m during the day (Irigoiien et al. 1997). Consequently, we assumed water from the upper layer

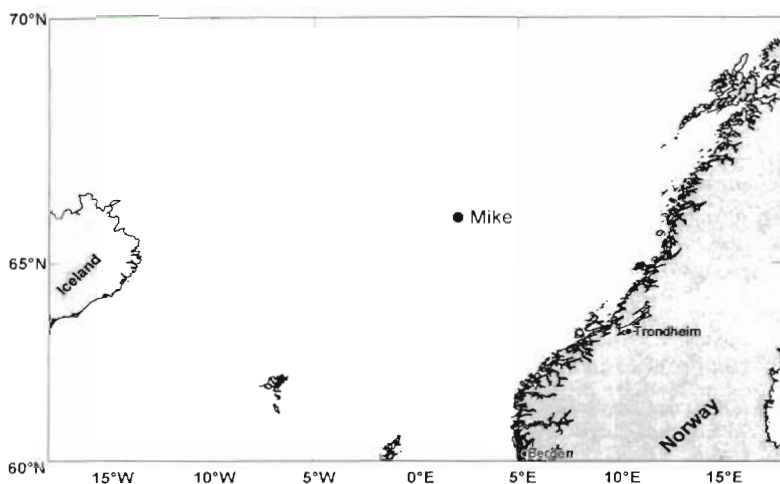


Fig. 1 The Norwegian Sea with the position of Stn M (Mike)

(5 m) to be representative of the feeding rates on heterotrophic microplankton. Feeding rates on ciliates and heterotrophic dinoflagellates were estimated by incubating 1 to 5 female *C. finmarchicus* in 1 l bottles filled with water from 5 m. Three to five replicates and 2 control bottles were incubated for 24 h at sea surface temperature and rotated intermittently. Two experiments were performed before the bloom, 2 during the bloom and 1 after the bloom. Samples of 200 ml were taken from incubation and control bottles at time 0 and time t and fixed with acid Lugol at 10% final concentration (Stoecker et al. 1994). Subsamples of 100 ml were settled (Utermöhl) and counted with an inverted microscope. Only experiments in which the reduction in ciliate numbers from the control to the grazing bottle was less than 40% were considered for calculation. To estimate ingestion rates, ciliates were measured and the carbon content was calculated from cell volume using a factor of $0.21 \text{ pg C } \mu\text{m}^{-3}$ (Ohman & Runge 1994). *Mesodinium* sp., a ciliate which is considered to be mixotrophic (having chl *a*), forms a significant fraction of the ciliate population and should appear in the gut fluorescence measurement. However, as the C:chl *a* ratio for *Mesodinium* is likely to be very different from that for phytoplankton and as high as 250 (Harbour pers. comm.), and considering also that ciliate ingestion appeared to be minor in comparison with phytoplankton, we took the conservative approach of including *Mesodinium* in the ciliate ingestion. Heterotrophic dinoflagellates were separated from autotrophic forms according to taxonomical considerations (Lessard & Swift 1986, Burkill et al. 1993). Filtration and ingestion rates in the incubations were calculated following Frost (1972).

Ciliate and heterotrophic dinoflagellate abundance were measured in the same way from 5 m samples taken on 19 occasions throughout the sampling period.

Meteorological data (air temperature, wind speed and direction) and wave height (measured with a shipborne wave recorder MK 4 system) were kindly provided by the captain of the weather ship 'Polar-front' (Stn M).

RESULTS

Hydrography

Weekly measurements to 1000 m: For the first period of our sampling program, the 35 psu salinity isohaline, which defines Atlantic water in the Norwegian Sea, was at about 300 m, with a strong intrusion of deeper water by the beginning of April (>100 m). From the end of April to June the 35 psu isohaline was about 400 m deep. Some oscillations in the depth of the Atlantic water layer could be detected but none were as strong as the one measured in the previous period. A strong gradient in temperature was related to the interface between Atlantic waters and waters of mixed Atlantic and Arctic origin. The 35 psu isohaline corresponded to a temperature of 3 to 4°C as previously described by Mosby (1950). These hydrological features indicate that all of the measurements presented in this work were carried out in Atlantic waters.

Daily measurements to 200 m: The Atlantic water layer (200 m) at Stn M was generally well mixed (Fig. 2). By the middle of May, a thermocline started to develop at a depth around 30 to 50 m. Pronounced stratification was established by June with mixing restricted to the upper 30 m. The temperature at the surface (5 m) increased from 5.5°C in March to 8.3°C at the end of the sampling period. The onset of the thermocline was clearly related to changes in atmospheric conditions. By the beginning of May the air temperature started to increase from around 6°C to 8°C, wind speeds weakened from a mean value of around 20 to 25 knots to less than 15 knots and the wave height decreased from values ranging from 2 to 4 m to values around 1 m.

Pigment distribution

The chl *a* concentration remained very low ($<0.5 \mu\text{g l}^{-1}$) during March and April (Fig. 3). The phytoplankton bloom occurred by 10 May (Fig. 3) and its maximum

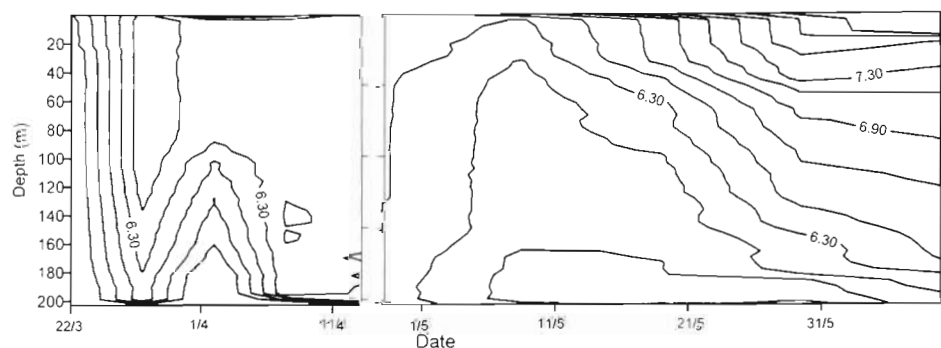


Fig. 2. Temperature (°C) profiles (0 to 200 m) at Stn M from 22 Mar to 9 Jun 1997. Data from 13 to 28 April are missing due to technical problems with the CTD

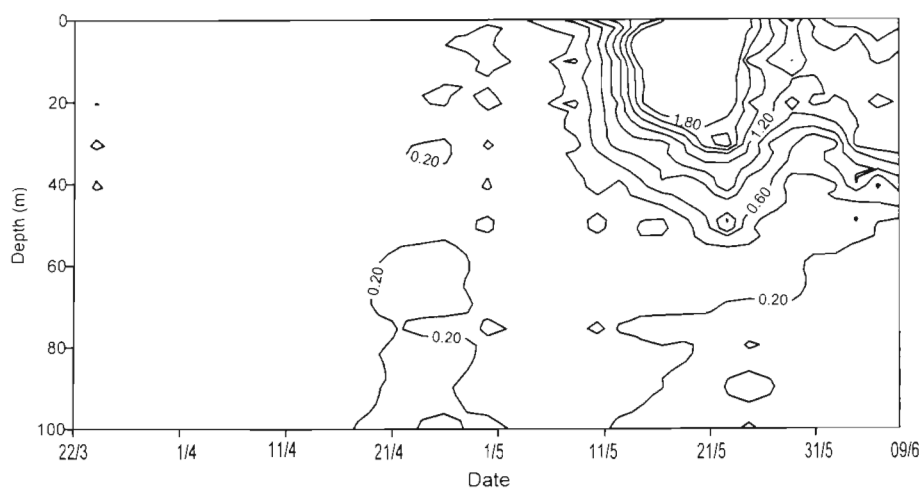


Fig. 3. Vertical distribution of chl *a* (0 to 100 m) at Stn M from 22 Mar to 9 Jun 1997

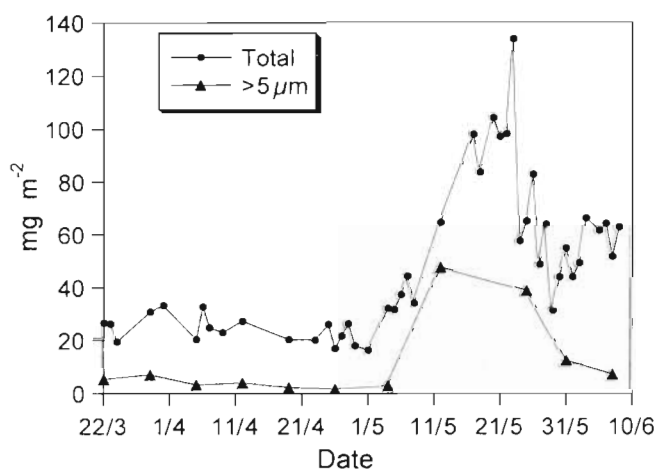


Fig. 4. Integrated (0 to 100 m) total chl *a* (●) and fractionated (>5 µm) chl *a* (▲) at Stn M from 22 Mar to 9 Jun 1997

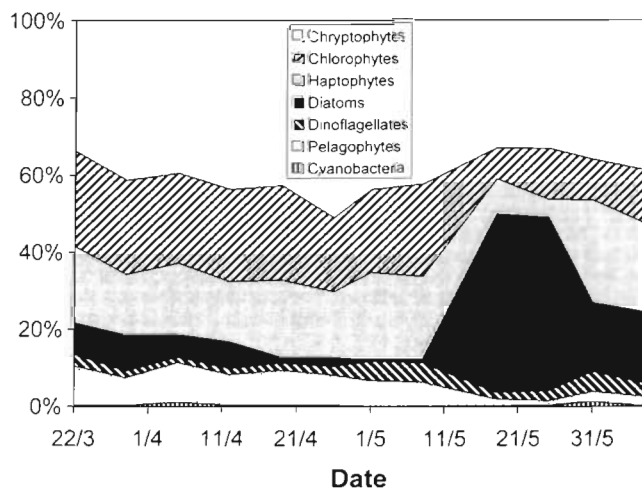


Fig. 5. Percentage contribution of the different phytoplankton groups to chl *a* for integrated values from surface to 60 m

(3 µg l⁻¹) coincided with the onset of stratification. The bloom appeared to be restricted to the upper 30 m; waters deeper than 40 m showed lower concentrations of chl *a* (<0.4 µg l⁻¹). The chl *a* concentration decreased by 25 May to remain around 1.5 µg l⁻¹ in the upper layer. The percentage of chl *a* greater than 5 µm was low in the March to mid May period, <20%, but increased significantly during the phytoplankton bloom, reaching 80% at 30 m (Fig. 4).

Fig. 5 presents the contributions of the different phytoplankton groups in terms of chl *a* to the integrated (0 to 60 m) chl *a* concentration. The percentage contribution of different phytoplankton groups was constant for the March to April period with a dominance of green algae (~40%), haptophytes (~30%) and cryptophytes (~25%).

Diatoms (~30%), cryptophytes (~30%) and dinoflagellates (~15%) were dominant during the bloom. After the bloom small flagellates became predominant again (Fig. 5). Chl *a* measured by fluorometry and by HPLC were well correlated: HPLC chl *a* = 1.03 Fluo chl *a* - 0.06 ($r^2 = 0.9$, $p < 0.05$, $n = 74$).

Consistent with phytoplankton dynamics, the results will be presented in 3 periods: pre-bloom (22 March to 10 May), during the bloom (11 May to 29 May) and post-bloom (30 May to 9 June).

Particulate carbon and nitrogen

TPC concentration decreased from the end of March to April and increased again during the bloom. TPC concentration ranged from 137 µg l⁻¹ by mid April at 100 m to 390 µg l⁻¹ by the end of May at 10 m. TPN followed the same pattern with values ranging from 18 µg l⁻¹ by mid April at 100 m to 51 µg l⁻¹ by the end of May at 10 m. The C:N ratio measured at different depths ranged from 6 to 8.2 with a mean value of 7.2 and did

not show any trend in relation to depth, season or phytoplankton concentration.

TPC was related to chl *a* by $TPC = 190.34 + 62 \text{ chl } a$ ($r^2 = 0.44$, $p < 0.01$, $n = 92$). The intercept of this equation indicates a high proportion of carbon unrelated to phytoplankton. After subtracting the phytoplanktonic carbon (with the slope of the previous regression) from the total particulate carbon, $185 \mu\text{g l}^{-1}$ not related to phytoplankton remained before the bloom, $206 \mu\text{g l}^{-1}$ during the bloom and $170 \mu\text{g l}^{-1}$ after the bloom. However, the differences are not significant (Mann-Whitney, $p > 0.05$) and this residual carbon does not appear to be related to other factors like depth or chl *a* concentration.

Heterotrophic microplankton

The mean ciliate biomass increased from $0.36 \mu\text{g C l}^{-1}$ ($1.4 \text{ cells ml}^{-1}$) before the bloom to $4 \mu\text{g C l}^{-1}$ ($7.9 \text{ cells ml}^{-1}$) during the bloom, decreasing again after the bloom to a mean value of $1.4 \mu\text{g C l}^{-1}$ ($1.3 \text{ cells ml}^{-1}$) (Fig. 6). Before the bloom the population was largely dominated by *Strombidium* type ciliates, comprising 96% of the total population. However they decreased to 85% during the bloom and 63% after the bloom. *Mesodinium* type ciliates increased significantly to 13% during the bloom and 35% after the bloom.

The mean concentration of heterotrophic dinoflagellates decreased from $1.1 \text{ cells ml}^{-1}$ ($0.6 \mu\text{g C l}^{-1}$) before the bloom to $0.4 \text{ cells ml}^{-1}$ ($0.1 \mu\text{g C l}^{-1}$) and to $0.13 \text{ cells ml}^{-1}$ ($0.01 \mu\text{g C l}^{-1}$) after the bloom. In terms of percentage the dominant groups were small peridiniids (45 to 70%), *Gyrodinium* (13 to 16%) and *Katodinium* (10 to 20%).

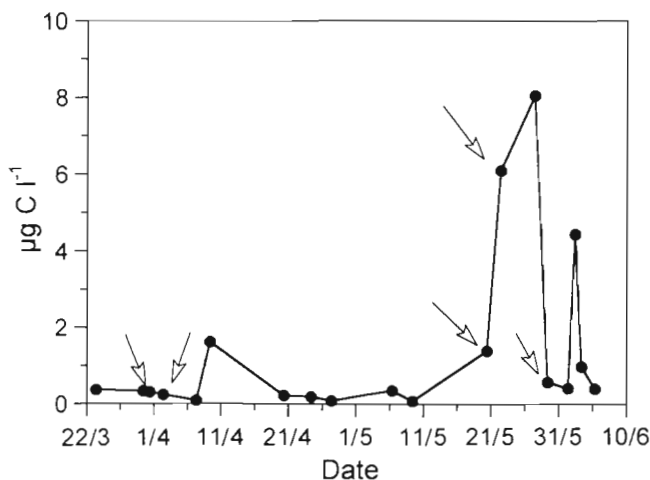


Fig. 6. Time course of the carbon concentration of ciliates (●) at 5 m depth from 22 Mar to 9 Jun 1997. Arrows indicate when experiments on ciliate ingestion were done

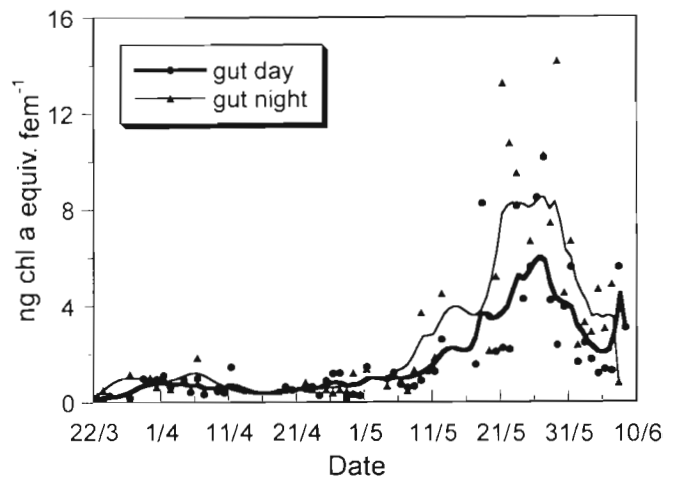


Fig. 7. *Calanus finmarchicus*. Time course of gut fluorescence at Stn M from 22 Mar to 9 Jun 1997. (●) Day values; (▲) night values. Lines represent smoothed data

Table 1. *Calanus finmarchicus* females. Mean and standard error (SE) of the day and night gut fluorescence values for the pre-bloom, bloom and post-bloom periods and probability of significant difference tested with a Mann-Whitney test

	Day		Night		Difference p
	Mean	SE	Mean	SE	
Pre-bloom	0.7	(0.06)	0.9	(0.15)	$p = 0.20$
Bloom	4.5	(0.76)	7.8	(1.3)	$p = 0.02$
Post-bloom	2.8	(0.54)	3.7	(0.57)	$p = 0.20$

Gut fluorescence

Gut fluorescence values were related to 100 m integrated chl *a* ($r^2 = 0.39$, $p < 0.05$ for daytime data and $r^2 = 0.30$, $p < 0.05$ for night-time data), with low values from March to April, a significant increase during the bloom and a decrease after the bloom (Fig. 7, Table 1). On average gut pigment levels were higher during the night than during the day but the difference was only significant during the bloom (Fig. 7, Table 1).

Feeding rates on phytoplankton

The mean phytoplankton ingestion rates estimated from gut fluorescence are presented in Table 2. When plotted against chl *a*, either integrated or in the surface, ingestion does not seem to reach saturation (Fig. 8). When using total chl *a* values, filtration rates ranged from 23 to $294 \text{ ml ind.}^{-1} \text{ d}^{-1}$ with a mean value of $88 \text{ ml ind.}^{-1} \text{ d}^{-1}$ before the bloom, from 41 to $357 \text{ ml ind.}^{-1} \text{ d}^{-1}$ with a mean value of $157 \text{ ml ind.}^{-1} \text{ d}^{-1}$ during the bloom and from 49 to $140 \text{ ml ind.}^{-1} \text{ d}^{-1}$ with a mean

Table 2. *Calanus finmarchicus* females. Mean phytoplankton and ciliate ingestion rates for the pre-bloom, bloom and post-bloom periods expressed in ngC fem.⁻¹ d⁻¹ and as percentage of the carbon body weight. In parentheses, the standard error of the mean for the phytoplankton ingestion is given

	Phytoplankton ingestion (ngC fem. ⁻¹ d ⁻¹)	% of body carbon	Ciliate ingestion (ngC fem. ⁻¹ d ⁻¹)	% of body carbon	% ciliates/ phytoplankton
Pre-bloom	1433 (190)	2.3	32	0.05	2
Bloom	14295 (2016)	30	836	1.8	6
Post-bloom	7587 (915)	14	226	0.4	3

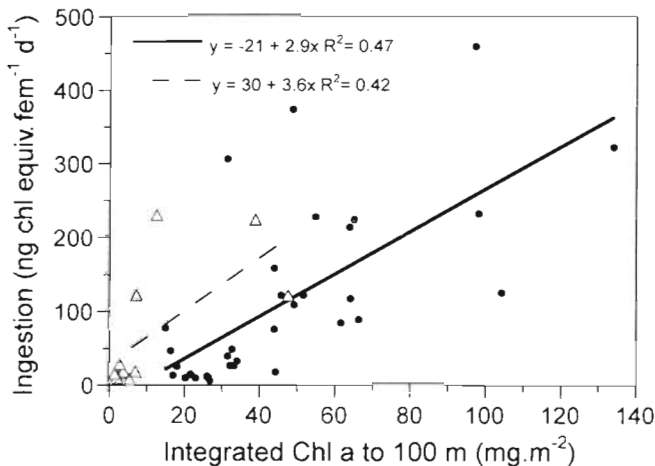


Fig. 8. *Calanus finmarchicus*. Relationship between upper 100 m integrated chl a concentration and chl a ingestion at Stn M. (●) Total chl a; (Δ) > 5 μm chl a

value of 106 ml ind.⁻¹ d⁻¹ after the bloom. If we consider only chl a > 5 μm, filtration values ranged from 97 to 903 ml ind.⁻¹ d⁻¹ with a mean value of 420 ml ind.⁻¹ d⁻¹ before the bloom, from 59 to 187 ml ind.⁻¹ d⁻¹ with a mean value of 123 ml ind.⁻¹ d⁻¹ during the bloom and from 680 to 761 ml ind.⁻¹ d⁻¹ with a mean value of 721 ml ind.⁻¹ d⁻¹ after the bloom.

From zooplankton biomass data (Klenke unpubl.) the grazing impact in the upper 100 m was estimated to be about 1% of the phytoplankton standing stock before the bloom, 15% during the bloom and 5% after the bloom.

Feeding rates on heterotrophic microplankton

Clearance rates on ciliates were high, ranging from 74 to 545 ml fem.⁻¹ d⁻¹ (Fig. 9), with ingestion values from 8.5 to 56 ngC fem.⁻¹ d⁻¹ before the bloom, 739 to 933 ngC fem.⁻¹ d⁻¹ during the bloom and 226 ngC fem.⁻¹ d⁻¹ after the bloom (Fig. 9).

Clearance rates on heterotrophic dinoflagellates ranged from 54 to 221 ml fem.⁻¹ d⁻¹, but

due to the low concentration in the water carbon ingestion was low, from 14 to 73 ngC fem.⁻¹ d⁻¹.

Carbon content and C:N ratio

The carbon content of adult females in the population decreased significantly during the pre-bloom period, remained constant during the bloom and increased slightly after the bloom (Fig. 10a). The C:N ratio follows the same pattern with a reduction from values of around 8 at the beginning of the sampling period to values of around 4 at the end of the pre-bloom period (Fig. 10b). Neither the N content (mean value 10.9 mgN fem.⁻¹) nor the prosome length of the females (mean value 2.5 mm) showed significant variations during the sampling period.

DISCUSSION

The phytoplankton bloom at Stn M appears to be clearly related to the onset of the thermocline in the upper layer. Increase in the compensation depth and

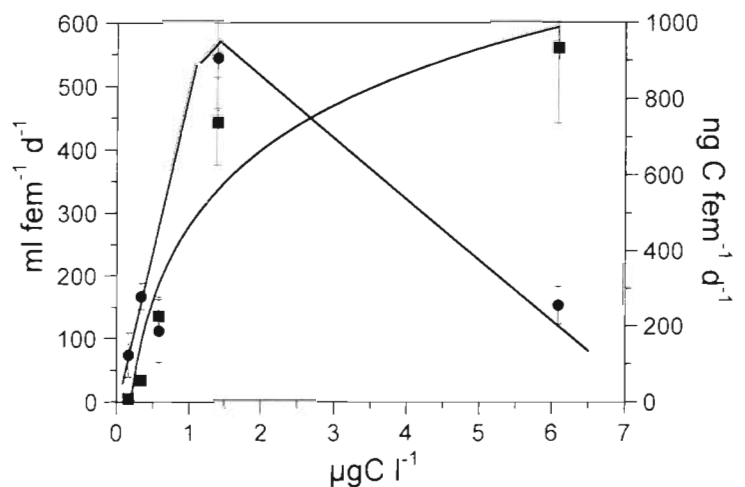


Fig. 9. *Calanus finmarchicus*. Ingestion (■) and filtration (●) rates of females feeding on ciliates as a function of ciliate concentration. Vertical bars indicate standard error of the mean

stability have long been recognised as decisive factors in the spring bloom development at Stn M (Sverdrup 1953, Halldal 1953). This is due to a reduction in the mixing depth/euphotic depth ratio as a consequence of stratification (Sverdrup 1953).

The bloom was also characterized by a change in the composition and cell size of the phytoplankton population from small flagellates and green algae to a predominance of diatoms (mainly *Rhizosolenia delicatula*).

It is generally believed that cells smaller than 5 µm are not available to *Calanus* (Marshall & Orr 1955) and in fact Gifford et al. (1995), in the North Atlantic, showed that the impact of *C. finmarchicus* grazing on cells smaller than 20 µm was negligible. Nevertheless, during our study, even taking the conservative approach of considering the animals feeding all the time in the maximum of chl *a*, the filtration rates on >5 µm chl *a* appear to be extremely high before and after the bloom, only comparable to the values obtained by Paffenhöfer (1971) with *C. helgolandicus* feeding on *Gymnodinium splendens* (60 µm maximum width dinoflagellate). Those unrealistic results suggest that at low chl *a* concentrations small cells should also be considered as a possible food source.

Only during the bloom were night-time gut fluorescence levels significantly higher than daytime values. For practical reasons, daily sampling times were limited and it is difficult to determine how representative the gut fluorescence measured at 09:00 and 21:00 h was of the maximum night and minimum day values, with the increasing day length from March to June. However, as the study was done during a period when the day length was increasing, the effect of higher light levels for the 'night' sample was likely to have been a reduction in the gut fluorescence, so the measured difference during the bloom is likely to be smaller than the real one, rather than an artifact. Mechanisms controlling diel feeding rhythms are still not well understood but risk of predation and hunger have been proposed as the most relevant factors. Johnsen & Jacobsen (1987) suggested that diel feeding rhythms and vertical migration reflect a trade-off between 2 conflicting interests: avoiding the increased risk of predation when feeding (Tiselius et al. 1997) and risking starvation (Huntley & Brooks 1982). Results on this subject are contradictory, with a number of studies providing evidence that food limitation

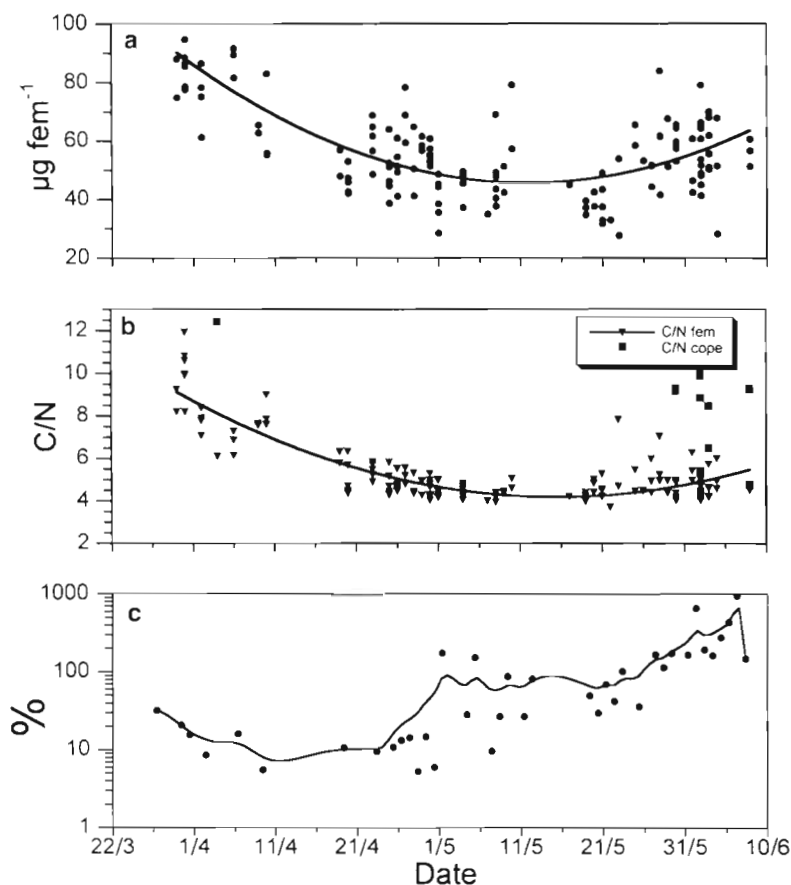


Fig. 10. *Calanus finmarchicus*. Time course (a) of female carbon content, (b) C:N ratio and (c) percentage of carbon requirements for egg production covered by phytoplankton ingestion at Stn M from 22 Mar to 9 Jun 1997. Squares in (b) represent C:N values for CIV and CV copepodites in the same samples. Fitted lines are $y = 2.81 \times 10^5 - 0.019x + 3.26 \times 10^{-11}x^2$ ($r^2 = 0.46$, $n = 145$) for carbon content (a) and $y = 2.89 \times 10^5 - 0.002x + 3.3 \times 10^{-12}x^2$ ($r^2 = 0.73$, $n = 145$) for C:N ratio (b). In (c) the line represents smoothed data

may alter or suppress diel migratory or feeding rhythms (Boyd et al. 1980, Huntley & Brooks 1982, Dagg 1985, Dagg & Walser 1987) whereas other studies show that feeding rhythms are maintained at low food concentration (Dagg & Grill 1980, Simard et al. 1985, Drits et al. 1990, Durbin et al. 1990). Our results seem to confirm the previous hypothesis with night gut contents on average 40% higher during the bloom against 20% before and after the bloom.

Gut fluorescence and ingestion rates measured during this study were within the range reported in the literature for *Calanus finmarchicus* (Tande & Båmstedt 1985, Smith & Lane 1988, Tiselius 1988, Ohman & Runge 1994, Cowles & Fessenden 1995, Durbin et al. 1995, 1997). An important controversy remains about the percentage of pigments destroyed in the gut of the copepods, with values ranging from 0 to 95% (see review in Pasternak 1994). On the other hand, when

Table 3. *Calanus finmarchicus* females. Egg production rate (EPR), standard error of the mean (SE), carbon requirements for egg production (see text for explanation), total ingestion (phytoplankton + ciliates) and percentage of the carbon requirements covered by ingestion. Egg production data from Niehoff et al. (1998)

	EPR (SE) (eggs fem. ⁻¹ d ⁻¹)	Carbon for EPR (ng C fem. ⁻¹ d ⁻¹)	Ingestion chl <i>a</i> + ciliates (ng C fem. ⁻¹ d ⁻¹)	% I/EPR
Pre-bloom	7.9 (0.7)	6380	1465	23
Bloom	24.8 (2.6)	19000	15130	80
Post-bloom	3 (0.6)	2300	7800	340

directly comparing different methods to estimate feeding, reliable results are obtained with gut fluorescence (Baars & Fransz 1984, Tiselius 1988, Peterson et al. 1990, see also Pasternak 1994). As an example, the ingestion measured here was equal to or higher than the ingestion calculated from incubation experiments during the same cruise which was 1.1, 15.4 and 2 % of the carbon body weight per day for the pre-bloom, bloom and post-bloom periods respectively (Meyer-Harms et al. unpubl.). In addition, if the chl *a* ingestion was seriously underestimated, one would expect low filtration rates because of not taking into account the result of an important part of the activity. On the contrary, measured filtration rates on phytoplankton were rather high and a significantly higher ingestion at the same chl *a* concentration would lead to unrealistic filtration rates even if estimated on total chl *a*. In fact, we observed an ingestion of 2 % of the body carbon weight per day at chl *a* concentrations lower than the previously estimated feeding threshold for *C. finmarchicus* by radioactive tracer methods (Daro 1980). However, it must be taken into account that due to some of the flaws in the methods (inadequate diel sampling, gut clearance rate estimated from the temperature or possible changes in the C:chl *a* ratio) the ingestion values must be considered as a range or approximate values rather than absolute values.

In order to estimate whether ingestion (phytoplankton + ciliates) was enough to maintain egg production, we estimated carbon requirements for the different periods from egg production rates measured at the same time as the ingestion measurements (Niehoff et al. 1998), assuming a carbon content of 230 ng C egg⁻¹ and a gross growth efficiency of 30 % (Hirche 1996) (Table 3, Fig. 10c). If, during the bloom, measured ingestion (phytoplankton + ciliates) nearly covered carbon requirements and post-bloom ingestion was in excess, pre-bloom ingestion was clearly not enough to cover egg production carbon requirements (Table 3).

The number of experiments on ciliate ingestion was low and could have been a source of error; however,

the sampling for the ciliate concentration was more intensive and the estimates correspond to those found in the literature (see Table 1 in Tiselius 1989). Moreover, heterotrophic contribution to the diet corresponds with that found by Ohman & Runge (1994) at similar ciliate concentration, 3.2 to 5.1 % of the total diet with 2.4 to 3.3 ciliates ml⁻¹.

The pattern of both carbon content and C:N ratio, which closely follow the percentage of carbon requirements covered by phytoplankton ingestion

(Fig. 10), suggests that an important percentage of the egg production carbon requirements before the bloom came from lipid storage. The decrease in carbon content is important, about 47 % in a period of 50 d, but still lower than that reported by Ohman & Runge (1994) in conditions of total starvation, ~17 % of the total lipids in 3.5 d. The C:N ratio changed from values typical for Arctic or Antarctic species to values close to those of temperate coastal species without, or with very low, lipid storage (Ikeda 1974).

Similar situations where the carbon content and C:N ratio or the lipid storage decreased in a similar way before the phytoplankton bloom have been reported for *Calanus finmarchicus* (Tande 1982) and for Antarctic species such as *C. propinquus* or *Metridia gerlachei* (Hagen & Schnack-Schiel 1996). Niehoff & Hirche (1996) conclude that vitellogenesis 1 is a slow process fuelled by internal lipid storage whereas vitellogenesis 2 is a fast process requiring external inputs. Hagen & Schnack-Schiel (1996) for *C. propinquus* and *M. gerlachei* and Plourde & Runge (1993) for *C. finmarchicus* also suggested that gonad formation and maturation were fuelled by internal energy reserves, but that major egg-laying activities would probably rely on external sources. This is in agreement with the results of Tande (1982) where the decrease in carbon content and C:N ratio coincided with the development of the gonads in CV and females but the final gonad maturation stage in females was only reached in April coinciding with the phytoplankton bloom.

Those previous results seem to indicate that carbon ingestion, either of phytoplankton or microzooplankton, is necessary for the final gonad maturation. It can be hypothesized that egg production should be the result of 2 factors: previous lipid storage, which has a reproductive potential and is represented by the decrease of both carbon content and C:N ratio (Tande 1982, this work), and instantaneously available food or actual ingestion, which will explain the relation between ingestion (or chl *a* concentration) and egg production rate frequently observed (Hirche et al. 1991, 1997, Niehoff et al. 1998) and will provide the

required external inputs for vitellogenesis 2. In this way the lack of agreement in the comparison between carbon requirements for egg production and ingestion before the bloom could be explained as due to not taking into account the use of lipid storage during vitellogenesis 1. Further, the difference between ingestion and egg production after the bloom probably contributes to the deposition of lipid storage as shown by the increase in C:N ratio. Unfortunately, estimation of the percentage contribution from lipid storage to egg production from the data we collected is difficult because gonad maturation in *Calanus finmarchicus* begins at stage V (Niehoff & Hirche 1996), so estimates of the contribution of lipids to egg production would have to follow the decrease in lipid storage for stage CV as well. Furthermore, the gross growth efficiency for phytoplankton ingestion is assumed to be around 0.3, but nothing is known about the efficiency of transforming storage lipids (wax-esters) into egg lipids (triacylglycerols) (Sargent & Falk-Petersen 1988).

Another possible source of carbon frequently neglected in the open sea is detritus. During our study TPC not related to phytoplankton was around $200 \mu\text{g l}^{-1}$, which in terms of phytoplankton would be a saturating concentration for *Calanus pacificus* (Frost 1972). Such high concentrations are not unusual. In the North Atlantic, Weeks et al. (1993) found TPC concentrations ranging from 120 to $170 \mu\text{g l}^{-1}$ where the sum of phytoplankton, bacteria and zooplankton did not exceed 25% of the TPC. In the English Channel, Holligan et al. (1984) measured detritus concentrations ranging from 102 to $394 \mu\text{g l}^{-1}$ and even in an oligotrophic sea like the Mediterranean the amount of POC (particulate organic carbon) not related to chl *a* seems to be around $200 \mu\text{g l}^{-1}$ or higher (see Table 1 and Fig. 4 in Saiz et al. 1992). However, the bulk of this detrital carbon in the open sea does not appear in microscopic analysis and is considered to be formed by 'structureless' material or 'marine snow' Paffenhöfer & Strickland (1970) showed that this natural detritus was not ingested by *Calanus helgolandicus*. Furthermore, during our study egg production was clearly related to the phytoplankton concentration and to the phytoplankton ingestion (Niehoff et al. 1998) whereas the amount of 'detritus' remains constant. So, it is unlikely that detritus plays an important role in the ingestion of *C. finmarchicus* in the Norwegian Sea.

Finally, the estimates given in this and other articles consider the metabolism (e.g. assimilation, gross growth efficiency) of the copepods to be the same at low food concentrations as at high concentrations. However, Landry & Hassett (1985) showed for *Calanus pacificus* that parameters like feeding potential, digestive enzyme activity or assimilation efficiency increase in response to chronically low food, suggesting that

before the bloom copepods can use the ingested carbon in a more efficient way than during and after the bloom.

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