

## Selective feeding on natural phytoplankton by *Calanus finmarchicus* before, during, and after the 1997 spring bloom in the Norwegian Sea

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### Abstract

Selective feeding by the calanoid copepod *Calanus finmarchicus* was investigated during a 3-month study in spring 1997 at a permanent station in the Norwegian Sea (Sta. M, 66°N, 02°E). Phytoplankton biomass increased from 317 ng chlorophyll *a* (Chl *a*) liter<sup>-1</sup> in the prebloom phase to 2,095 ng liter<sup>-1</sup> during the bloom and declined after the bloom to 1,260 ng Chl *a* liter<sup>-1</sup>. In the prebloom phase, clearance rates of *C. finmarchicus* females were between 22 and 100 ml copepod<sup>-1</sup> d<sup>-1</sup>, while during the bloom, they ranged from 75 to 92 ml copepod<sup>-1</sup> d<sup>-1</sup>, with a decline in the postbloom phase (41 ml copepod<sup>-1</sup> d<sup>-1</sup>). After the phytoplankton bloom, the *C. finmarchicus* population was dominated by copepodid stages CIV and CV, with clearance rates ranging from 7 to 23 ml copepod<sup>-1</sup> d<sup>-1</sup>. Grazing rates of adult females on the phytoplankton standing stock were low in the prebloom phases (5–23 Chl *a* copepod<sup>-1</sup> d<sup>-1</sup>, respectively), increased during the bloom from 82 to 219 ng Chl *a* copepod<sup>-1</sup> d<sup>-1</sup>, and declined after the bloom (64 ng Chl *a* copepod<sup>-1</sup> d<sup>-1</sup> for adult females and 7–27 ng Chl *a* copepod<sup>-1</sup> d<sup>-1</sup> for copepodid stages CIV and CV). *C. finmarchicus* showed a selection for diatoms throughout the study period and for dinoflagellates, before and after the spring bloom, despite the low concentration of both groups in the pre- and postbloom phases. During the postbloom period, no differences were observed in the selective feeding behavior of the copepodid stages compared to the adults. The contribution of diatoms to the overall phytoplankton biomass was 8 and 14% in the pre- and postbloom periods, respectively, while dinoflagellates were ≤3%. Haptophytes (dominated by *Phaeocystis pouchetii*) and cryptophytes were ingested according to their abundance. Avoidance of cyanobacteria (*Synechococcus* spp.), pelagophytes, and “green algae” was observed throughout the study period.

The calanoid copepod *C. finmarchicus* dominates zooplankton biomass in the North Atlantic (Williams et al. 1994; Cowles and Fessenden 1995). It is a key biological component of temperate ecosystems and plays an intermediary role between phytoplankton and fisheries variability in this area (Runge 1988). The Marshall and Orr monograph (1955a), the review by Huntley (1988) and, more recently, Harris (1996) have all considered the feeding biology of *Calanus*. Much of the earlier literature on copepod feeding behavior focused on size selection of phytoplankton in the field (e.g., Poulet 1973, 1974; Gamble 1978) and more recently, on small-scale interactions between feeding behavior and anatomical structure (Paffenhöfer 1988). From recent investigations (e.g., Støttrup and Jensen 1990; Jónasdóttir 1994; Jónasdóttir et al. 1995; Pond et al. 1996), it has been established that food quality affects copepod production and ultimately, production at higher trophic levels. A detailed understanding of food quality will depend on an appreciation of the role of individual groups, and even species, of phytoplankton in nutrition (Harris 1996). Up to now, little in-

formation has been available on selective feeding of *C. finmarchicus* on natural phytoplankton assemblages (Ohman and Runge 1994; Nejstgaard et al. 1997).

The aim of the present study was to estimate selective feeding by *C. finmarchicus* during prebloom, bloom, and postbloom conditions in the Norwegian Sea. Feeding rates were estimated, using high-performance liquid chromatography (HPLC)-determined pigment concentrations, in simulated in situ incubation experiments, during a 3-month study on the weathership at Sta. M. Head and Harris (1994) first used this method to describe selective feeding by different size-fractionated zooplankton off the coast of Morocco. A modification of the method was described by Meyer-Harms and von Bodungen (1997) in feeding experiments with *Acartia bifilosa* in the Pomeranian Bight (Baltic Sea, Germany).

The Norwegian Sea is the major region of high abundance of *C. finmarchicus* in the NE Atlantic (Oceanographic Laboratory-Edinburgh 1973). This study reports the first time series of observations on the feeding behavior of *C. finmarchicus* at a deep-water station in this important center of the trans-Atlantic range. The investigation forms part of the TASC project, which is making an integrated Trans-Atlantic Study of *C. finmarchicus*.

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### Methods

The study was carried out at Sta. M (*Mike*), 66°N, 02°E, from 22 March to 10 June 1997, onboard the Norwegian weathership *Polarfront*. This position has been occupied as a permanent weather station since 1948 (Fig. 1).

Water for the weekly grazing experiments was collected, from 5-m depth, with a rosette water sampler fitted with 5 liters of Niskin (teflon spring) bottles. The water was gently

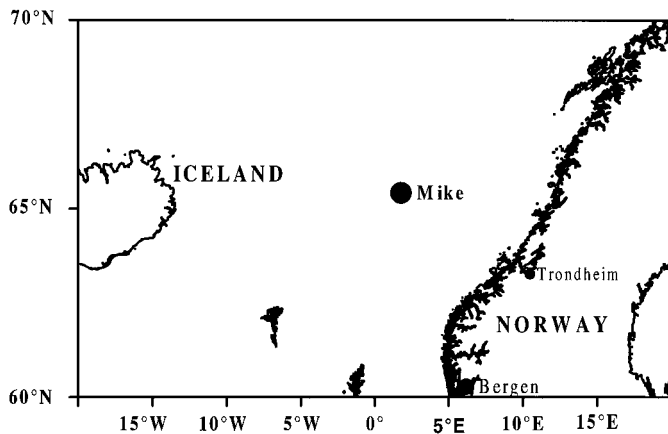


Fig. 1. Location of Sta. M (*Mike*) in the Norwegian Sea.

passed through a 500- $\mu$ m mesh to reduce the abundance of mesozooplankton before the incubation. A subsample for HPLC (2 liter) was filtered onto Whatman GF/F glass-fiber filters (47 mm in diameter) and stored in liquid nitrogen until further analysis in the laboratory.

**Pigment analysis by HPLC**—The frozen GF/F filters were extracted in 4 ml of 90% acetone by sonication and centrifugation. An aliquot (300  $\mu$ l) of the acetone extract was then mixed with 300  $\mu$ l of 1 M ammonium acetate and injected (100  $\mu$ l) onto a 3- $\mu$ m Shandon Hypersil<sup>®</sup> MOS2 (endcapped) C-8 (100  $\times$  4.6 mm) column. Pigments were separated at a flow rate of 1 ml min<sup>-1</sup> by a linear gradient programmed as follows (minutes, % solvent A, % solvent B): (0, 75, 25), (1, 50, 50), (20, 30, 70), (25, 0, 100), and (32, 0, 100). A detailed description of this method is given in Barlow et al. (1997). Solvent A consisted of 70:30 (v/v) methanol:1 M ammonium acetate, and solvent B was 100% methanol. This method allows a good separation of mono- and divinyl Chl *a* and *b* as well as zeaxanthin and lutein. The system consisted of a Shimadzu LC-6A pump with system controller (SCL-6B), absorbance detector (Shimadzu SPD-6AV) set at 440 nm, and a fluorescence detector (Shimadzu RF-535) set at excitation 415–435 nm and emission at 650–670 nm. Dual channel data collection and integration utilized Philips PU6000 software. The system was calibrated with pigment standards from the VKI Water Quality Institute. Pigments were identified by comparison with retention times of the standards and by on-line diode array spectroscopy using a Waters 990 diode array spectrophotometric detector.

**Calculation of pigment to Chl *a* ratios**—To estimate the contribution of the different phytoplankton groups to the total phytoplankton biomass in terms of Chl *a*, the CHEMTAX program was used. A detailed description of this program is given by Mackey et al. (1996, 1997). The calculation by CHEMTAX is based on the measured Chl *a* and the accessory pigment concentrations of suitable biomarkers of each algal class measured in subsamples of the grazing experiments (1) before the bloom ( $n = 37$ ), and (2) during and after the bloom ( $n = 27$ ).

**Zooplankton samples**—*C. finmarchicus*, used in the grazing experiments, were collected using a 50- $\mu$ m mesh WP2 net, towed vertically from 100 m to the surface. Immediately after capture, organisms were gently poured into 10-liter buckets with water from 5-m depth. Healthy individuals were then isolated under a stereomicroscope and transferred to grazing bottles.

**Simulated *in situ* incubations**—During the prebloom and bloom periods, five adult females were incubated in 1-liter bottles filled with natural seawater from 5-m depth (three replicates), and three bottles, without copepods, were used as controls. During the postbloom period, mainly copepodids stage IV or IV were used in the grazing experiments (10 copepods per bottle) as the abundance of adult females was very low. Bottles were kept in incubators under dim light at *in situ* temperature (the depth at which the incubation water had been collected) and were rotated intermittently during incubation (24 h). The temperature rose from 5.5°C in March to 8.3°C by the end of the sampling period in June. At the end of each experiment, the incubation water (including the water from the controls) was passed through a 500- $\mu$ m mesh to isolate the copepods. These were then transferred gently in filtered seawater to check for mortality. No mortality occurred in any of the experiments. Subsamples of the incubation water (600–700 ml) were collected from each bottle. Because of the low phytoplankton concentrations during the study, all three subsamples from the grazing experiments were filtered through a single Whatman GF/F glass-fiber filter (47 mm in diameter), which was stored in liquid nitrogen until subsequent analysis in the laboratory. The same procedure was conducted with the subsamples from the control bottles. Hence, each filter represented a mean value of the replicates of control and grazing bottles.

**Calculation of grazing impact**—The Chl *a* concentration was used to express the grazing impact on the total phytoplankton biomass. The taxon-specific grazing impact on the total phytoplankton crop was estimated using HPLC-determined accessory pigment distributions: The Chl *a* equivalent (eqv.) of each algal group, calculated by CHEMTAX, at the beginning and end of each experiment for the subsamples from the control and grazing bottles, was used to calculate the taxon-specific grazing rates according to Frost (1972).

During the investigation, random samples of feces were analyzed by HPLC, as the residual pigment remaining in fecal pellets may influence calculation of grazing rates (Head and Harris 1994). The copepods were incubated under the same experimental conditions as described above, and the feces, produced in the incubation bottle, were pipetted on Whatman GF/F filters and used for pigment analysis by HPLC. In all of the samples analyzed ( $n = 4$ , pre- and post-bloom period,  $n = 3$ , during the bloom), both chlorophylls and marker pigments were almost completely transformed into degradation products, and, in contrast to the investigation reported by Nelson (1989), we could not clearly identify the carotenoids separated by HPLC. The pigment concentration in these samples was always  $<0.05$  ng liter<sup>-1</sup> (200–500 pellets) for both Chl *a* and the sum of the detected marker pigments. Hence, the fecal pellets, which were produced dur-

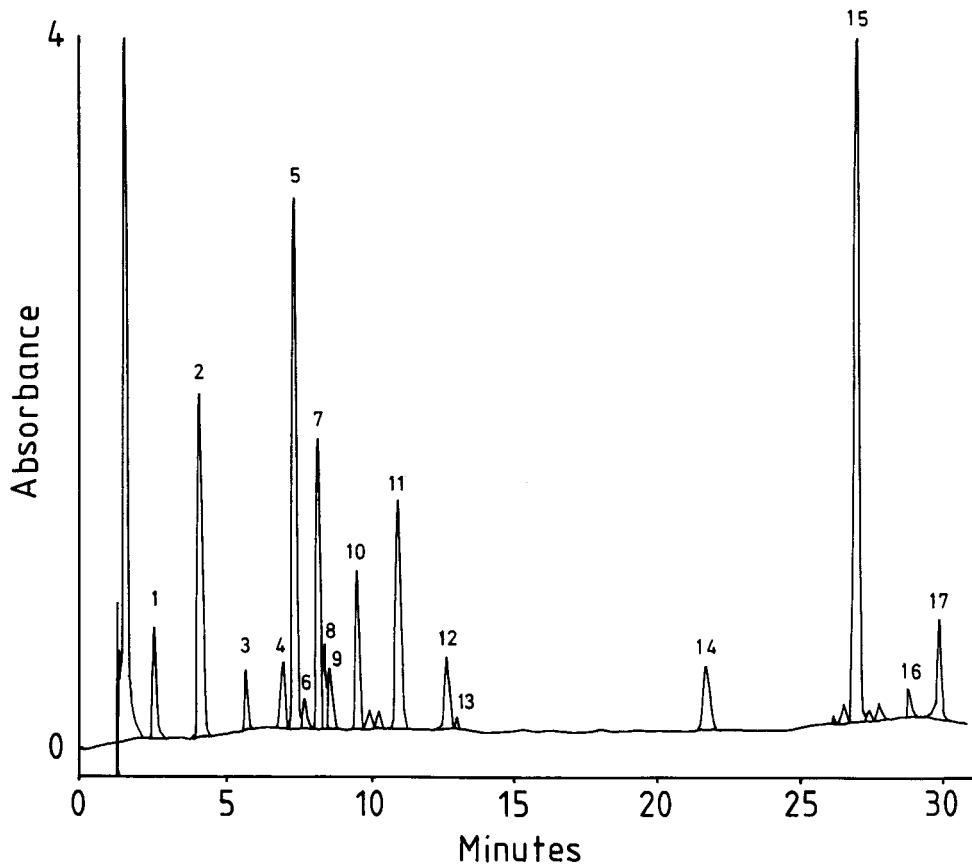


Fig. 2. HPLC chromatogram, with the typical pigment pattern, of water from 5-m depth (27.05.1997). 1. Chl  $c_3$ , 2. Chl  $c_{1+2}$ , 3. peridinin, 4. 19'-butanoyloxyfucoxanthin, 5. fucoxanthin, 6. neoxanthin, 7. 19'-hexanoyloxyfucoxanthin, 8. prasinoxanthin, 9. violaxanthin, 10. diadinoxanthin, 11. alloxanthin, 12. zeaxanthin, 13. lutein, 14. Chl  $b$ , 15. Chl  $a$ , 16. phaeophytin  $a$ , and 17.  $\alpha$ - and  $\beta$ -carotene.

ing incubation and isolated on the filter with the residual phytoplankton cells at the end of the experiment, did not influence the calculated grazing rates. These results are in agreement with the findings of Head (1992), Head and Harris (1994, 1996), and Harradine et al. (1996), who observed complete transformation and destruction of phytoplankton pigments after gut passage in *Calanus*.

*Estimation of selective feeding behavior*—Selective feeding behavior by *C. finmarchicus* during the investigation period was characterized using the chi-square ( $\chi^2$ ) goodness-of-fit test (Cowles 1979), as described in detail by Sokal and Rohlf (1969). The frequency distribution of food types in the diet was compared with that in the environment. Selective feeding was indicated by a significant divergence of the distribution (Kleppel et al. 1996).

Food selection on specific phytoplankton groups was quantified using the selectivity index (SI)  $\alpha$ , according to Chesson (1978). The calculation of  $\alpha$  is based on the relative contribution of the estimated phytoplankton biomass of each phytoplankton group (in Chl  $a$  eqv.) at the beginning of each experiment and the relative contribution of the ingested phytoplankton groups to total ingestion. According to Chesson (1978),  $\alpha = 0.5$  indicates nonselective feeding,  $\alpha > 0.5$  in-

dicates a preference for a phytoplankton group, and  $\alpha < 0.5$  indicates discrimination against an algal group. A two-way analysis of variance (ANOVA) was used to identify differences between calculated selectivity indices of *C. finmarchicus* for each phytoplankton group within and between the different phases of the bloom. The differences between specific groups during the investigation were tested with a post hoc least square difference (LSD) test.

## Results

*Temporal variation of pigments in the grazing experiments*—A representative absorbance chromatogram of the pigments detected in the incubation water of the grazing experiments is given in Fig. 2. The Chl  $a$  concentration, generally used as an indicator of phytoplankton biomass, remained low in the prebloom phase during March and April (213–750 ng liter<sup>-1</sup>). After 9 May, as the phytoplankton bloom developed, the Chl  $a$  concentration steadily increased and reached a maximum on 22 May (2,863 ng liter<sup>-1</sup>). Following the phytoplankton bloom at the end of May, the Chl  $a$  concentration ranged between 1,165 and 1,727 ng liter<sup>-1</sup> (Fig. 3).

The HPLC method employed is not capable of separating

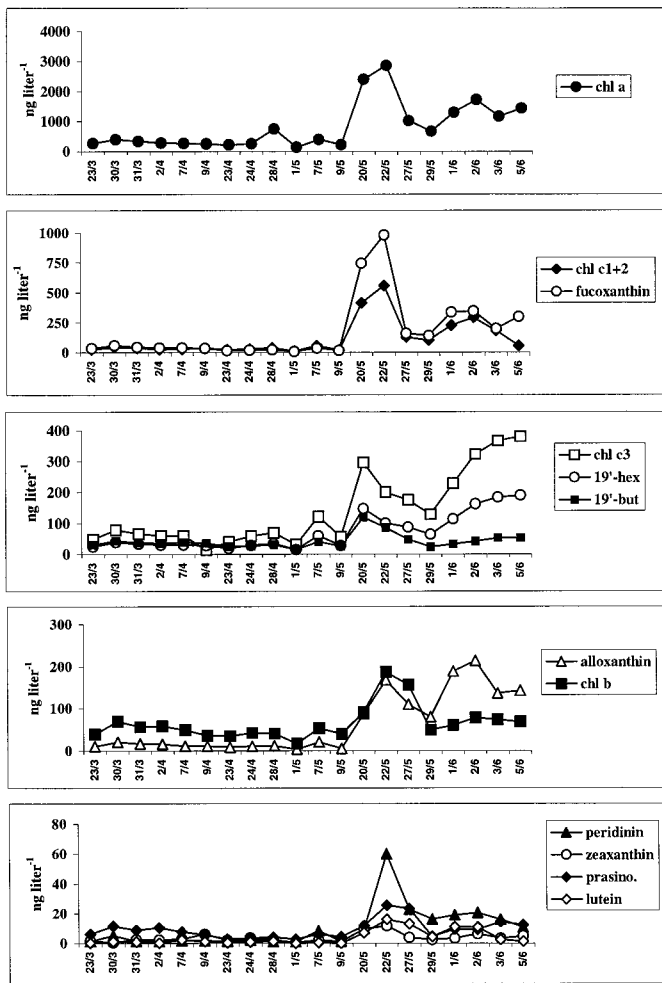


Fig. 3. Temporal variation (date/month of sampling) in the concentrations of Chl *a*, Chl *c*<sub>1+2</sub>, fucoxanthin, Chl *c*<sub>3</sub>, 19'-hexanoyloxyfucoxanthin (19'-hex), 19'-butanoyloxyfucoxanthin (19'-but), alloxanthin, Chl *b*, peridinin, and zeaxanthin at 5-m depth (at which the incubation water was collected) during the study in the Norwegian Sea.

Chl *c*<sub>1</sub> from Chl *c*<sub>2</sub>, and the corresponding peak is referred to as Chl *c*<sub>1+2</sub>. The pigment “Chl *c*<sub>1+2</sub>” is present in pelagophytes, cryptophytes, diatoms, dinoflagellates, and haptophytes (Barlow et al. 1993; Andersen et al. 1996). It was highly correlated with fucoxanthin ( $r^2 = 0.972$ ,  $n = 20$ ,  $P < 0.001$ ), with highest concentrations of both pigments on 22 May (fucoxanthin 983 ng liter<sup>-1</sup>, Chl *c*<sub>1+2</sub> 558 ng liter<sup>-1</sup>). These results suggest that the majority of Chl *c*<sub>1+2</sub> originated from diatoms (Fig. 3). Both Chl *c*<sub>1+2</sub> and fucoxanthin followed the same pattern as Chl *a*. The pigment 19'-hexanoyloxyfucoxanthin (19'-hex) was, with fucoxanthin, the dominant carotenoid in the grazing experiments and is commonly used as a biomarker for haptophytes (Andersen et al. 1996). Some haptophyte species also contain, in addition to 19'-hex, fucoxanthin or fucoxanthin plus 19'-butanoyloxyfucoxanthin (19'-but; Jeffrey and Wright 1994). The concentration of 19'-hex increased with Chl *a* as the bloom developed but, in contrast to fucoxanthin, 19'-hex peaked on 20 May (Fig. 3). The pigment 19'-but followed the same

pattern as 19'-hex until the bloom developed (20 May,  $r^2 = 0.902$ ,  $n = 13$ ,  $P < 0.001$ ), but thereafter, it was not correlated with 19'-hex. The pigment Chl *c*<sub>3</sub> followed a similar pattern to 19'-hex ( $r^2 = 0.922$ ,  $n = 20$ ,  $P < 0.001$ ) and acted as a complementary biomarker for haptophytes.

Concentrations of Chl *b* ranged from 17 to 70 ng liter<sup>-1</sup> in the prebloom phase and increased during the bloom to 187 ng liter<sup>-1</sup> on 22 May (Fig. 3). Postbloom Chl *b* ranged from 50 to 79 ng liter<sup>-1</sup>.

Low values of alloxanthin were observed in the prebloom phase (4–21 ng liter<sup>-1</sup>), but this pigment increased steadily during the investigation (Fig. 3), reaching a maximum on 2 June (214 ng liter<sup>-1</sup>).

Lutein (0.0–2.3 ng liter<sup>-1</sup>), zeaxanthin (0.4–6.0 ng liter<sup>-1</sup>), peridinin (1.0–8.0 ng liter<sup>-1</sup>), and prasinoxanthin (2.7–11.6 ng liter<sup>-1</sup>) remained at low concentrations during the prebloom phase (Fig. 3). Only zeaxanthin did not increase during the study period (Fig. 3).

*Contribution of selected phytoplankton groups to Chl a biomass*—The contribution of selected algal classes to total phytoplankton standing stock was estimated from the pigment data before, during, and after the bloom using CHEMTAX. Pelagophytes were not included in the calculation of pigment:Chl *a* ratios before the bloom (Table 1a), when the pigment was associated with haptophytes (*see above*), and no pelagophyte cells were identified by microscopy (Harbour pers. comm). Lutein, the biomarker for chlorophytes, was also not used for the calculation of pigment:Chl *a* ratios because very low pigment concentrations (*see Fig. 3 and above*) may result in errors using CHEMTAX (Wright pers. comm.). Prasinoxanthin, the dominant carotenoid in prasinophytes, could not be completely separated from violaxanthin (Fig. 2) and was therefore not used in the CHEMTAX algorithm. Hence, Chl *b* was used as a marker for “green algae” (chlorophytes and prasinophytes). The absence of divinyl Chl *a* indicated that prochlorophytes did not contribute to Chl *b*.

The mean percentage contributions of selected algal groups to estimated Chl *a* are given in Fig. 4. Phytoplankton biomass was dominated in the prebloom phase by “green algae” and haptophytes (39 and 37%, respectively). During the bloom, diatoms increased to 47% of the Chl *a* biomass. Haptophytes, cryptophytes, and diatoms were the dominant phytoplankton groups in the postbloom phase (39, 33, and 14%, respectively). The contribution of dinoflagellates, cyanobacteria, and pelagophytes to phytoplankton standing stock was low throughout the study (1–3%, 0.01–0.5%, and 1–2%, respectively).

Microscopic cell counts of preserved field samples indicated that microflagellates and diatoms were the major components of the phytoplankton community (Harbour pers. comm.). The main species of diatoms before and after the bloom were *Pseudonitzschia* spp. (40 × 2 μm) and *Thalassiosira* spp. (10–20 μm in diameter), while during the bloom, *Rhizosolenia delicatula* (40 × 8 μm) was the dominant species. Among the haptophytes, only *P. pouchetii* could be identified. Dinoflagellates were dominated by a number of unidentified small peridinin (12 × 8 μm) and *Prorocentrum* species (10 × 8 μm), and the cryptophytes

Table 1. Accessory pigment:Chl *a* ratios calculated by CHEMTAX for the subsamples collected from the grazing experiments (a) in the prebloom period, and (b) during bloom and postbloom conditions (per, peridinin; fuco, fucoxanthin; but, 19'-butanoyloxyfucoxanthin; hex, 19'-hexanoyloxyfucoxanthin; all, alloxanthin; zeax, zeaxanthin). Pelagophyte ratios were not calculated during the prebloom conditions (*see text for details*).

Phytoplankton group	Pigments								
	Chl <i>c</i> <sub>3</sub>	Chl <i>c</i> <sub>1+2</sub>	per	but	fuco	hex	all	zeax	Chl <i>b</i>
(a):									
Diatoms	0.000	0.118	0.000	0.000	0.607	0.000	0.000	0.000	0.000
Dinoflagellates	0.000	0.268	0.500	0.000	0.000	0.000	0.000	0.000	0.000
Haptophytes	0.162	0.221	0.000	0.329	0.155	0.600	0.000	0.000	0.000
"Green algae"	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.017	0.432
Cyanobacteria	0.000	0.000	0.000	0.000	0.000	0.000	0.000	2.500	0.000
Cryptophytes	0.000	0.060	0.000	0.000	0.000	0.000	0.300	0.000	0.000
(b):									
Diatoms	0.000	0.141	0.000	0.000	0.450	0.000	0.000	0.000	0.000
Dinoflagellates	0.000	0.268	0.500	0.000	0.000	0.000	0.000	0.000	0.000
Haptophytes	0.330	0.089	0.000	0.076	0.412	0.596	0.000	0.000	0.000
Pelagophytes	0.250	0.254	0.000	0.933	0.624	0.000	0.000	0.000	0.000
"Green algae"	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.022	0.569
Cyanobacteria	0.000	0.000	0.000	0.000	0.000	0.000	0.000	2.500	0.000
Cryptophytes	0.000	0.254	0.000	0.000	0.000	0.000	0.354	0.000	0.000

were dominated by numerous unidentified cryptomonads ( $10 \times 5 \mu\text{m}$ ). Cyanobacteria were solely represented by *Synechococcus* spp., and the majority of microflagellates could not be associated with a specific algal class.

*Taxon-specific grazing impact of C. finmarchicus on the phytoplankton standing stock*—In the prebloom phase, clearance rates (CRs) of *C. finmarchicus* females were between 22 and 100 ml copepod<sup>-1</sup> d<sup>-1</sup>, while during the bloom, they ranged between 75 and 92 ml copepod<sup>-1</sup> d<sup>-1</sup>, with a decline in the postbloom phase (41 ml copepod<sup>-1</sup> d<sup>-1</sup>; Fig. 5). After the phytoplankton bloom, the *C. finmarchicus* population was dominated by copepodid stages CIV and CV. Their CRs ranged between 7 and 23 ml copepod<sup>-1</sup> d<sup>-1</sup>.

Ingestion rates (IRs) showed a similar pattern, with low rates in the prebloom period (5–23 ng Chl *a* copepod<sup>-1</sup> d<sup>-1</sup>)

and high values during the bloom (82–219 ng Chl *a* copepod<sup>-1</sup> d<sup>-1</sup>; Fig. 5). During the postbloom phase, the IR of adult females was 64 ng Chl *a* copepod<sup>-1</sup> d<sup>-1</sup>, while the IRs of copepodid stages CIV and CV ranged between 6 and 28 ng Chl *a* copepod<sup>-1</sup> d<sup>-1</sup> (Fig. 5).

Taxon-specific CRs and IRs are presented in Fig. 6; Table 2. CRs and IRs of *C. finmarchicus* on cyanobacteria and pelagophytes were mainly negative for all three phases of the bloom, indicating that there was no grazing on this group. During the 3-month investigation, *Calanus* showed the lowest CRs on "green algae" and the lowest IRs on "green algae" and dinoflagellates (Fig. 6; Table 2).

In the prebloom phase, the highest CR was on dinoflagellates and diatoms (109 and 79 ml copepod<sup>-1</sup> d<sup>-1</sup>, respectively). CRs on the other groups were, with the exception of the "green algae" (13 ml copepod<sup>-1</sup> d<sup>-1</sup>), similar, with val-

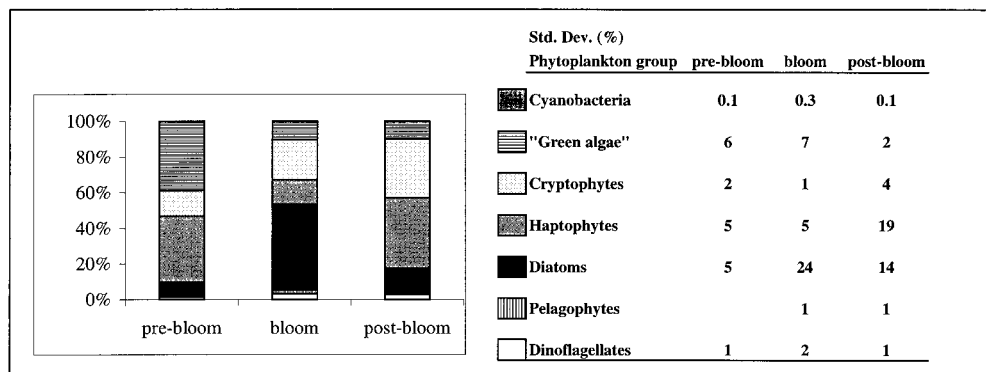


Fig. 4. Mean value (left panel) and SD of the mean (right panel) of the relative contribution of the different phytoplankton groups to the total Chl *a* biomass at 5 m during prebloom (23 March–9 May,  $n = 11$ ), bloom (20 May–27 May,  $n = 3$ ), and postbloom (29 May–3 June,  $n = 5$ ) conditions in the Norwegian Sea. Cyanobacteria as a percentage of the total phytoplankton biomass ranged between 0.01 and 0.5% during the investigation period and are therefore not visible in the figure.

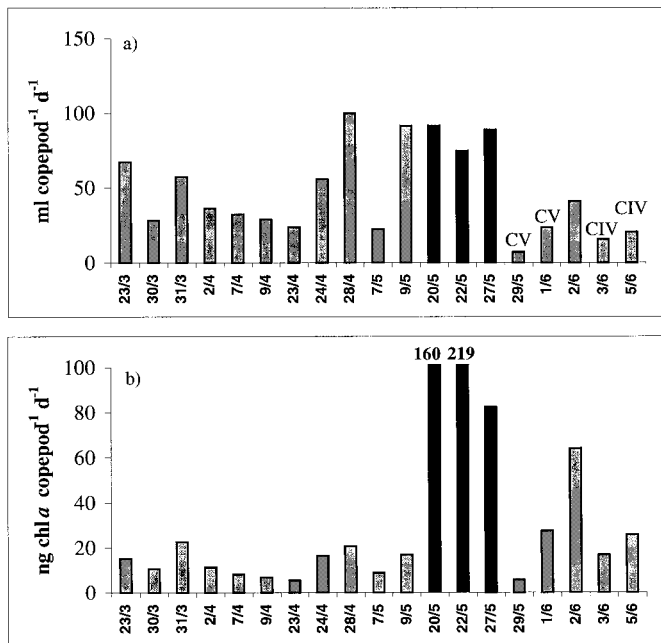


Fig. 5. Clearance rate (a) and Chl *a* ingestion rate (b) of *C. finmarchicus* in simulated in situ experiments (with natural phytoplankton assemblages from 5-m depth) before (23 March–9 May), during (black columns 20 May–27 May), and after the bloom (29 May–5 June) in the Norwegian Sea (date/month of sampling).

ues ranging between 33 and 46 ml copepod<sup>-1</sup> d<sup>-1</sup> (Table 2). During the bloom, the highest CRs were on diatoms (133 ml copepod<sup>-1</sup> d<sup>-1</sup>) followed by cryptophytes, dinoflagellates, and haptophytes (86, 69, and 66 ml copepod<sup>-1</sup> d<sup>-1</sup>, respectively). In the postbloom phase, the pattern was similar to that determined before the bloom. The highest CR was on dinoflagellates (182 ml copepod<sup>-1</sup> d<sup>-1</sup> for adult females, 56 and 35 ml copepod<sup>-1</sup> d<sup>-1</sup> for copepodid stages CIV and CV, respectively; Table 2), followed by diatoms, cryptophytes, and haptophytes, respectively (Table 2).

During the prebloom period, the highest IR was observed for haptophytes (4 ng Chl *a* eqv. copepod<sup>-1</sup> d<sup>-1</sup>), while during the bloom, the highest IR was estimated on diatoms (123 ng Chl *a* eqv. copepod<sup>-1</sup> d<sup>-1</sup>). After the bloom period, the IR for adult females of *C. finmarchicus* was highest on diatoms, whereas it was highest by copepodid stages CIV on haptophytes and CV on cryptophytes (Table 2).

**Selective feeding of *C. finmarchicus* on the phytoplankton standing stock**—The frequency of selective feeding by *C. finmarchicus* was high. Differences between the composition of phytoplankton in the environment and in the diet were significant in all experiments (Table 3). Diatoms were positively selected, and selection on dinoflagellates occurred, especially in the pre- and postbloom periods (Table 4). According to the CRs and IRs on cyanobacteria and pelagophytes described above, *C. finmarchicus* avoided these algal classes together with “green algae,” in contrast to the other phytoplankton groups (Table 4).

Haptophytes and cryptophytes were ingested in proportion to their abundance throughout the study. During the bloom,

which was mainly composed of diatoms (*Rhizosolenia* spp.), *C. finmarchicus* selected this group (Table 4). The feeding behavior in the postbloom phase was similar to the prebloom period (Table 4), with no differences between copepodid stages CIV and CV and adult females. Feeding on dinoflagellates was only significantly different between bloom and nonbloom conditions (Tables 4, 5).

## Discussion

**Phytoplankton distribution**—In regions of the oceans in which microflagellates are an important component of the phytoplankton community, biomarkers have been shown to be useful tools for describing phytoplankton composition (Barlow et al. 1993; Andersen et al. 1996). According to Millie et al. (1993), microflagellates cannot usually be determined by microscopic cell counting, at either the group or species level (Meyer-Harms and von Bodungen 1997; this study). The phytoplankton distribution in the Norwegian Sea (Weslawski et al. 1991) is similar to the one reported by Gifford et al. (1995) in the North Atlantic during May. These authors also found dominance of the haptophyte *P. pouchetii* and of diatoms of the genus *Rhizosolenia*, *Nitzschia*, and *Thalassiosira*.

In the last 10 yr, it has been established that pigment to Chl *a* ratios vary with changing irradiance (e.g., Gieskes et al. 1988; Brunet et al. 1993; Letelier et al. 1993; McManus 1995; Waterhouse and Welschmeyer 1995; Jeffrey et al. 1997; Meyer-Harms and von Bodungen 1997). A classical approach to calculate habitat specific pigment ratios from field data is to use multiple regression analysis (MRA; e.g., Gieskes and Kraay 1983; Gieskes et al. 1988; Barlow et al. 1993; Bustillos-Guzmán et al. 1995; Meyer-Harms and von Bodungen 1997). This approach is based on measured Chl *a* and marker pigment concentrations and is a useful tool when a specific carotenoid is related to a single algal class. Unfortunately, this is not always the case (Mackey et al. 1997). Fucoxanthin, for instance, is generally used as a marker for diatoms, but it is also present in some pelagophytes and haptophytes. Therefore, it is not possible to differentiate between these algal classes by MRA. The CHEMTAX program used in our calculations is able to disentangle this problem because it takes into account biomarkers with multiple sources. The results presented show that the pigment:Chl *a* ratios calculated using CHEMTAX are within the range of values shown by Mackey et al. (1996, 1997) and the ratios calculated by MRA (e.g., Gieskes and Kraay 1983; Gieskes et al. 1988; Barlow et al. 1993; Bustillos-Guzmán et al. 1995; Meyer-Harms and von Bodungen 1997). The pigment signatures of the phytoplankton composition found in this study are comparable to the ones in the NE Atlantic during spring (Barlow et al. 1993).

**Grazing of *C. finmarchicus***—In general, it is difficult to characterize the food of copepods in natural seawater (Dagg et al. 1982). This work reports the first in situ time-series study of selective feeding behavior of *C. finmarchicus* in the open ocean. The estimated IRs on the phytoplankton biomass are in the same range of values found in the literature (Table 6), which supports the usefulness of a pigment-based

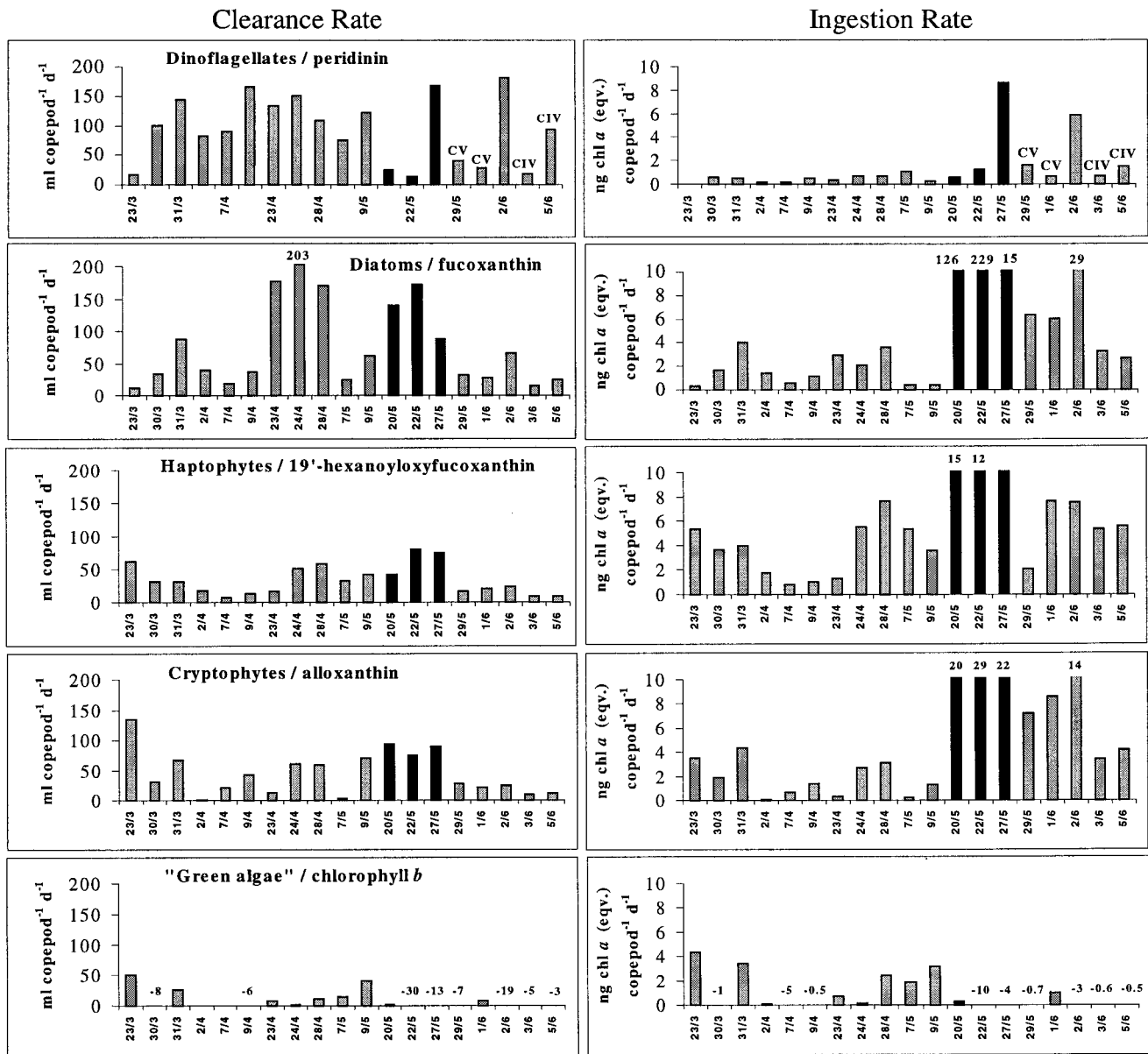


Fig. 6. Clearance rate (left) and ingestion rates (right) in terms of Chl *a* eqv. of *C. finmarchicus* (females and copepodids stages V and IV) on the different phytoplankton groups in the incubation water (natural seawater assemblage from 5-m depth) before (23 March–9 May), during (black columns 20 May–27 May), and after the spring bloom (29 May–5 June) in the Norwegian Sea (date/month of sampling).

Table 2. Mean value of clearance (CR, ml copepod<sup>-1</sup> d<sup>-1</sup>) and ingestion rates (IR) in Chl *a* equivalents (eqv., ng Chl *a* eqv. copepod<sup>-1</sup> d<sup>-1</sup>) given in Fig. 6 of *C. finmarchicus* (adult females = F, copepodid stages CV and CIV) on the different phytoplankton groups in the prebloom, bloom, and postbloom phase during spring in the Norwegian Sea.

Phytoplankton group	Prebloom phase		Bloom phase		Postbloom phase					
					CR			IR		
	CR	IR	CR	IR	F	CV	CIV	F	CV	CIV
Dinoflagellates	109	0.5	69	3.5	182	35	56	5.9	1.1	1.1
Diatoms	79	1.7	133	123.1	66	30	20	28.5	6.2	3.0
Haptophytes	33	3.6	66	12.4	24	18	9	7.6	4.9	5.5
Cryptophytes	46	1.8	86	23.8	24	24	11	13.6	7.9	3.8
"Green algae"	13	0.8	-14	-4.6	-19	0.6	-4	-2.8	0.1	-0.5

Table 3. The chi-square ( $\chi^2$ ) goodness-of-fit test (Sokal and Rohlf 1969) between the composition of phytoplankton in the environment and in the diet.

Date of experiments (date/month)	$\chi^2$	Significance
23/3	16.7	$P < 0.01$
30/3	49.2	$P < 0.01$
31/3	21.5	$P < 0.01$
2/4	116.1	$P < 0.01$
7/4	116.9	$P < 0.01$
9/4	10.6	$P < 0.01$
23/4	46.9	$P < 0.01$
24/4	59.2	$P < 0.01$
28/4	35.8	$P < 0.01$
1/5	9.7	$P < 0.05$
7/5	18.0	$P < 0.01$
9/5	14.9	$P < 0.01$
20/5	24.3	$P < 0.01$
22/5	14.5	$P < 0.01$
27/5	49.5	$P < 0.01$
29/5	49.2	$P < 0.01$
1/6	11.5	$P < 0.01$
2/6	45.4	$P < 0.01$
3/6	32.0	$P < 0.01$
5/6	45.4	$P < 0.01$

technique in simulated in situ grazing experiments. Furthermore, IRs of *C. finmarchicus* determined in this study are also comparable to IRs measured by gut fluorescence (Tande and Båmstedt 1985; Smith and Lane 1988) (Table 7). After the phytoplankton bloom at the end of May, the *C. finmarchicus* population was dominated by copepodid stages CIV and CV, and their clearance and ingestion rates appeared, in agreement with Paffenhöfer (1971), to be lower than for adult females (Table 7). However, no differences were observed in the selective feeding behavior of the copepodid stages compared to the adults (Table 4).

Traditionally, copepods have been considered to be major grazers on phytoplankton (Nejstgaard et al. 1997). However, it has become increasingly apparent that microzooplankton is also an important component of the copepod diet (e.g., Stoecker and Capuzzo 1990; Kleppel 1993) and may support copepod egg production (Ohman and Runge 1994). During the same cruise, Irigoien et al. (1998) showed that IRs of *C. finmarchicus* on microzooplankton were low. The authors reported that the IRs on ciliates ranged from 9 to 56 ng C copepod<sup>-1</sup> d<sup>-1</sup> before the bloom, from 739 to 933 ng C copepod<sup>-1</sup> d<sup>-1</sup> during the bloom, and averaged 226 ng C copepod<sup>-1</sup> d<sup>-1</sup> after the bloom, while the IRs on heterotrophic dinoflagellates ranged between 14 and 73 ng C copepod<sup>-1</sup> d<sup>-1</sup> throughout the study period. Nevertheless, despite low ingestion rates on microzooplankton, this could possibly be an important nutritional component of the diet during periods of low food supply, because of its high organic content (Kleppel 1993). According to Poulet (1983), *C. finmarchicus* can use detritus as an additional food source to phytoplankton. Irigoien et al. (1998) reported, also for the weather ship Sta. M study, that egg production was clearly related to the

Table 4. Mean value and standard error of the mean of the selectivity coefficient  $\alpha$  for *C. finmarchicus* based on the relative contribution of the taxon-specific algal groups in the incubation water at the beginning of the grazing experiments and their relative contribution to the diet, in the different phases of the bloom in the Norwegian Sea (March–June 1997).

Phytoplankton group	Prebloom phase (n = 11)	Bloom phase (n = 3)	Postbloom phase (n = 5)
Dinoflagellates	0.75±0.06	0.39±0.21	0.73±0.07
Pelagophytes		0.16±0.16	0.06±0.04
Diatoms	0.66±0.06	0.69±0.05	0.66±0.02
Haptophytes	0.53±0.04	0.44±0.05	0.41±0.02
Cryptophytes	0.52±0.07	0.48±0.06	0.50±0.04
“Green algae”	0.18±0.06	0.01±0.01	0.07±0.07

phytoplankton concentration and to phytoplankton ingestion, whereas the amount of detritus remained constant. Therefore, it is argued that it is unlikely that detritus plays an important role in the ingestion of *C. finmarchicus* in the Norwegian Sea.

*Reasons for selection*—During our study, *C. finmarchicus* showed a positive selection for diatoms (throughout the study period) and dinoflagellates (during pre- and postbloom conditions). It has been known since the early work of Harvey (1937) that *Calanus* can feed selectively. However, the reasons for and mechanisms of a selective feeding behavior by *Calanus* are still uncertain (see reviews in Huntley 1988; Harris 1996). Algal size is usually considered to be one of the factors in selection by *Calanus* (Frost 1972), and in our case, it can certainly explain the selection on diatoms and dinoflagellates compared to the small flagellates. Selection on diatoms supports the classical view reported by Marshall and Orr (1955b), which is that *Calanus* is an effective grazer on diatoms. Even the early studies reported by Marshall (1924) showed that the gut contents of *C. finmarchicus* consisted chiefly of diatoms and dinoflagellates.

Selection on dinoflagellates before and after the bloom was higher than for diatoms, although this group was of minor importance in the natural population. The cell size of the majority of dinoflagellates in the incubation water was much less than the cell size of the dominant diatoms throughout the investigation (see Results). Experiments conducted by Cowles et al. (1988) have demonstrated that food selection by copepods can occur on the basis of food quality. Previous studies have shown that egg production is related

Table 5. Two-way ANOVA for differences between the selective behavior (calculated by selectivity index  $\alpha$ ) between specific groups during the study period in the Norwegian Sea from March to June 1997 (\*\*  $P < 0.001$ ; \*  $P < 0.05$ ).

Source of variation	df	MS	F	P level
(1) Phytoplankton groups	4	0.779	26.022**	0.000
(2) Investigation period (time)	2	0.096	3.221*	0.045
(1) × (2)	8	0.037	1.237	0.289

Table 6. Literature data of IRs in terms of carbon (C), Chl *a*, or percent of body carbon (% C) per copepod (cop<sup>-1</sup>) and day (d<sup>-1</sup>) of adult *C. finmarchicus* estimated by simulated in situ incubation experiments with similar Chl *a* concentrations (conc.) as in this study.

Area	Month	Chl <i>a</i> conc. (μl <sup>-1</sup> )	IR (cop <sup>-1</sup> d <sup>-1</sup> )	Reference
Greenland Sea (Fram Strait)	June/July	0.6	950 ng C, 0.2% C	Smith 1988
Gulf of St. Lawrence	June/July	0.3–0.7	2,400–9,300 ng C, 1.1–4.2% C	Ohman and Runge 1994
North Atlantic 59°N	May	1.3	115 ng Chl <i>a</i>	Gifford et al. 1995
Bergen (Norway)	May/June	0.2	12 ng Chl <i>a</i>	Nejstgaard et al. 1997
Norwegian Sea	March–June	0.3	13 ng Chl <i>a</i> , 637 ng C, 1.1% C	This study
		2.1	154 ng Chl <i>a</i> , 9,240 ng C, 15.4% C	
		1.3	64 ng Chl <i>a</i> , 2,688 ng C, 4.5% C	

to the quality of algae offered (Støttrup and Jensen 1990; Jónastóttir 1994; Jónastóttir et al. 1995). Since dinoflagellates have a higher volume-specific organic content than diatoms under the same growth conditions (e.g., Hitchcock 1982), they are increasingly recognized as being important in the diet of *Calanus* (Price et al. 1983; Gill and Harris 1987; Kleppel et al. 1991; Kleppel 1993).

In addition to cell size and food quality, recent research on selective feeding has shown that prey motility can also influence the feeding behavior of calanoid copepods (e.g., Saiz 1994; Saiz and Kiørboe 1995; Kiørboe et al. 1996; Kleppel et al. 1996). For example, *C. propinquus* from the Bellingshausen Sea showed a strong selection for motile cells, particularly small dinoflagellates, when phytoplankton biomass was low (52–174 ng Chl *a* liter<sup>-1</sup>; Atkinson 1995). An explanation for the selection behavior related to abundance and motility of the prey may be found in differences in the feeding mode of copepods. Saiz and Kiørboe (1995) and Kiørboe et al. (1996) reported that *Acartia tonsa* could switch between a suspension and an ambush feeding behavior. At low phytoplankton concentrations, feeding effort (clearance) is reduced. The copepods switch to ambush feeding, and motile prey, such as dinoflagellates or ciliates, are more important. In this feeding mode, copepods do not produce a feeding current; they sink slowly through the water column, and when motile prey are sensed by mechanoreceptors on the antennae, the copepods attempt to capture it.

According to Kleppel et al. (1996), such feeding behavior can provide 1–3% of body C d<sup>-1</sup>. However, when the prey is sufficiently abundant, e.g., during bloom conditions, the copepod generates a feeding current (suspension feeding; Kiørboe et al. 1996). The selection behavior of *C. finmarchicus* on dinoflagellates and diatoms found in this study supports the prey-switching theory described by Saiz and Kiørboe (1995) and Kiørboe et al. (1996).

Throughout the study period from March to June 1997, haptophytes dominated by *P. pouchetii* and cryptophytes were ingested by *C. finmarchicus* according to their abundance. The feeding behavior of calanoid copepods on *Phaeocystis* is unclear in many cases. Some studies have demonstrated ingestion (e.g., Tande and Båmstedt 1987), whereas others have inferred that *Phaeocystis* is not ingested by *Calanus helgolandicus* because of the gelatinous nature of some life-cycle phases under certain conditions (e.g., Bautista et al. 1992). Sargent and Falk-Petersen (1988) reported that *P. pouchetii* is a major constituent of the diet of *C. finmarchicus*. As shown by Estep et al. (1990), predation upon *P. pouchetii* is a function of the physiological state of the colonies.

Cyanobacteria, pelagophytes, and “green algae,” respectively, were avoided by *C. finmarchicus* during the study period. Johnson et al. (1982) reported similar findings. The authors showed that the cyanobacteria, *Synechococcus* spp., were not utilized by *C. finmarchicus*, and Latasa et al. (1997)

Table 7. Mean values of the Chl *a* concentrations (conc.) in the incubation bottles; IR and CR estimated in terms of Chl *a*, carbon (C), and % of body C of *C. finmarchicus* during the different phases of the phytoplankton bloom. The conversion to C was by using C:Chl *a* ratios based on Chl *a* concentrations measured by HPLC (this study) and C values based on cell volume carbon conversions from microscopic analysis of phytoplankton (kindly provided by D. Harbour). IR values in terms of % body C were calculated with a mean value for the investigation period of 60 μg C for *C. finmarchicus* females (F), 54 μg C for copepodid stage CV, and 27 μg C for copepodid stage CIV (Irigoiien et al. 1998).

	Prebloom phase	Bloom phase	Postbloom phase
Chl <i>a</i> (ng Chl <i>a</i> liter <sup>-1</sup> )	317	2,095	1,260
C:Chl <i>a</i> ratio	49	60	42
IR (ng Chl <i>a</i> copepod <sup>-1</sup> d <sup>-1</sup> )	13	154	64 (F), 22 (CV), 17 (CIV)
IR (ng C copepod <sup>-1</sup> d <sup>-1</sup> )	637	9,240	2,688 (F), 924 (CV), 714 (CIV)
IR (% of body C copepod <sup>-1</sup> d <sup>-1</sup> )	1.1	15.4	4.5 (F), 1.7 (CV), 2.6 (CIV)
CR (ml copepod <sup>-1</sup> d <sup>-1</sup> )	49	85	41 (F), 18 (CV), 15 (CIV)

reported avoidance of pelagophytes in microzooplankton grazing experiments. Støttrup and Jensen (1990) showed, in grazing experiments with *A. tonsa*, that egg production ceased entirely within 4 d when the copepods were fed with the chlorophyte *Dunaliella tertiolecta*, and Meyer-Harms and von Bodungen (1997) reported avoidance by *A. biflosa* of chlorophytes in the Pomeranian Bight (Germany).

The results of this study suggest that feeding of *Calanus* is influenced by a combination of different factors such as algae cell size, food quality, and abundance and motility of the prey. The study provides the first quantitative information on the diet and feeding behavior of *C. finmarchicus* before, during, and after the spring bloom in a key deep-water center of the trans-Atlantic range. The major advantage of our study is that IRs on phytoplankton can be differentiated at the level of major phytoplankton groups. The results presented are the first approach to measuring selectivity of *C. finmarchicus* under simulated field conditions by using a pigment-based technique, which is less time-consuming than cell counting. This technique allows a better interpretation of the utilization of available phytoplankton resources in comparison to traditional methods, which only measure bulk parameter such as Chl *a*. By exploiting this technique, it has been shown that *C. finmarchicus* selects diatoms throughout the entire study period and dinoflagellates before and after the bloom, despite the low concentration of both groups in the pre- and postbloom phases. In the future, to answer questions such as how selection and energy needs are related to each other, detailed studies involving parallel measurements covering a wide range of parameters (e.g., food composition, organic content of the food, ingestion, egg production, respiration, and excretion rates) are required. Such investigations will contribute to a better understanding of key organisms such as *C. finmarchicus*, which play an intermediary role between primary producers and fish populations.

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