Feeding of *Calanus finmarchicus* nauplii in the Irminger Sea

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ABSTRACT: Recent studies have shown that the passage from nauplius to copepodite is a key event in the population dynamics of *Calanus finmarchicus*. As a first step towards understanding if and how trophic interactions influence this event, we investigated the feeding of *C. finmarchicus* nauplii IV–VI in the Irminger Sea during spring and summer in a series of incubation experiments. Generally, feeding efficiencies were highest on large cells, whereas small flagellates were ingested at very low rates. Colonies of *Phaeocystis* sp. were not ingested. Among the larger cells, the diatoms *Chaetoceros pelagicus* and *Tropodineis* sp. and the ciliate *Strombidium* sp. were the main food sources. We observed a negative relationship between the percentage of diatoms in the food environment and the filtration rate on *Strombidium* sp. We therefore suggest that the combination of low feeding efficiency on small cells and the generally low concentrations of ciliates in oceanic waters explains why *C. finmarchicus* relies on phytoplankton blooms for recruitment from nauplius to the first copepodite stage.

KEY WORDS: *Calanus finmarchicus* nauplii · Feeding · Phytoplankton · Microzooplankton

INTRODUCTION

The copepod *Calanus finmarchicus* is a key species in the North Atlantic, often representing over 50% of the zooplankton biomass (Planque & Batten 2000). Due to their abundance, *Calanus* nauplii are a main food source for larvae of commercially important fish, i.e. cod, and of importance for their recruitment. The Irminger Sea between Iceland and Greenland is one of the major centres of *C. finmarchicus* distribution in the North Atlantic (Planque & Batten 2000).

Calanus finmarchicus overwinters at depth, and it is generally assumed that after returning to the surface in spring, it exploits the phytoplankton bloom for reproduction. This view has recently been challenged by studies in the Norwegian Sea showing that by using its lipid storage, *C. finmarchicus* is able to produce eggs before the bloom, when food concentration is still low

(Irigoien et al. 1998, Niehoff et al. 1999). However, a detailed analysis of the population structure during the same study in the Norwegian Sea showed that although eggs are produced before the bloom, the resulting nauplii only recruit to copepodites when coincident with the bloom (Hirche et al. 2001) and that before the bloom the death rate is higher than the birth rate (Ohman & Hirche 2001). These results suggest that the passage from nauplius to copepodite is a key event in the population dynamics of *C. finmarchicus*, and suggest that the phytoplankton bloom plays an important role in the success of naupliar development.

Unfortunately, our knowledge about *Calanus* nauplii feeding ecology is limited (Harris 1996). Only a few studies have examined their feeding and growth rates in the laboratory (Marshall & Orr 1956, Paffenhofer 1971, Fernandez 1979, Rey et al. 2001, Meyer-Harms et al. 2002) and survival in response to starvation (Lopez 1996). To
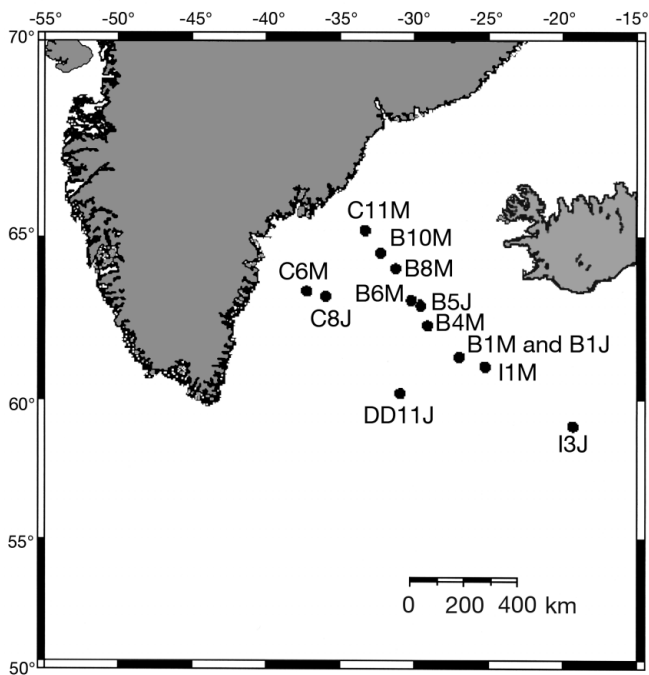
Fig. 1. Map of the study area

our knowledge only 1 article on feeding of *Calanus* nauplii under natural conditions has been published (Turner et al. 2001). In the present study, we examined *C. finmarchicus* naupliar feeding on natural particles for a wide range of food conditions in the Irminger Sea.

MATERIALS AND METHODS

We quantified feeding rates and selectivity of *Calanus finmarchicus* nauplii in a series of shipboard experiments carried out during RRS 'Discovery' Cruises D262 and D264 in spring and summer 2002 in the Irminger Sea. Experimental stations are presented in Fig. 1 and basic parameters for each station can be found in Table 1.

Naupliar feeding rates on the different nano- and microplanktonic groups (cells >2 μm) were quantified by incubating 15 to 25 *Calanus finmarchicus* nauplii, Stage IV to VI (mainly Stage V), in 200 ml bottles filled with water from the chl *a* maximum. Nauplii were sorted from vertical hauls at all stations. In each experiment, 3 replicate experimental and 3 replicate control bottles were in-

Table 1. Position and main characteristics of the experimental stations. SST: sea surface temperature

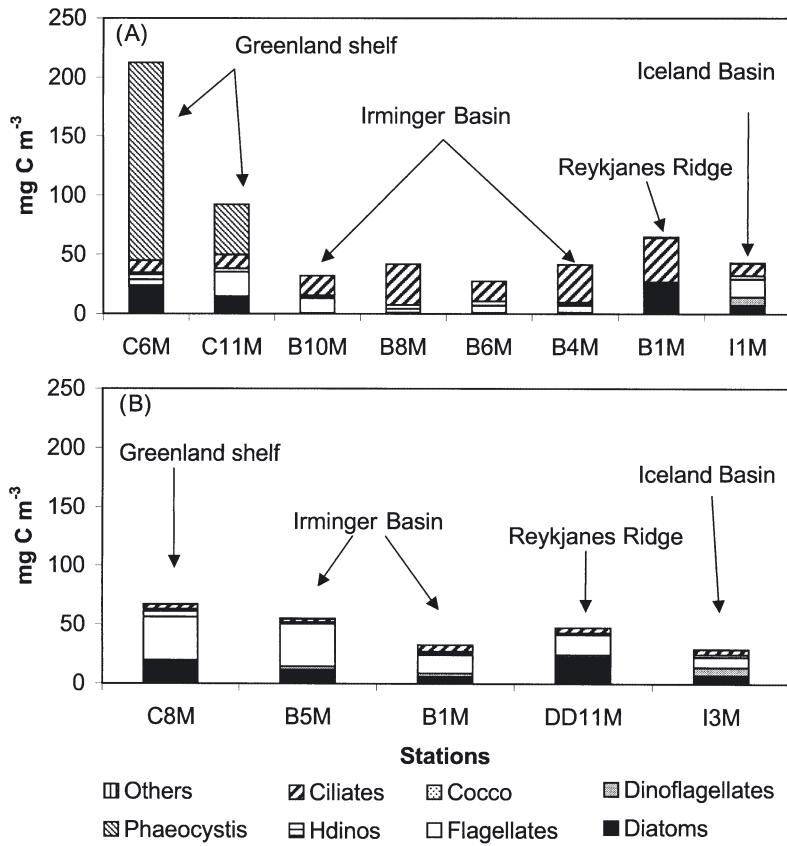| Stn	Date (d/mo/yr)	Position	SST (°C)	Surface salinity	Surface chl *a* (2 m) (mg m^{-3})	Experiment initial nano- and micro-plankton (mg C m^{-3})	Region (observations)
Spring cruise							
I1M	22/05/02	61° 08′ 95″ N 25° 26′ 04″ W	7.9	35.1	1.4	49	Iceland Basin
B1M	21/05/02	61° 40′ 70″ N 27° 02′ 46″ W	7.0	35.1	0.9	64.9	Reykjanes Ridge
B4M	20/05/02	62° 38′ 60″ N 29° 14′ 60″ W	6.8	35.1	0.9	41.4	Irminger Basin
B6M	19/05/02	63° 17′ 09″ N 30° 23′ 82″ W	7.1	35.1	0.8	27.6	Irminger Basin
B8M	18/05/02	64° 10′ 52″ N 31° 29′ 32″ W	6.9	35.1	0.6	41.9	Irminger Basin
B10M	17/05/02	64° 56′ 97″ N 32° 30′ 22″ W	5.6	34.7	1.4	32.3	Irminger Basin
C11M	16/05/02	65° 20′ 16″ N 33° 36′ 24″ W	7.9	35.2	1.1	92.3	Greenland shelfbreak
C6M	11/05/02	66° 44′ 38″ N 37° 29′ 36″ W	1.2	33.3	1.2	212	Greenland shelf (Partially ice covered; fresh water in surface)
Summer cruise							
I3J	30/07/02	59° 12′ 57″ N 19° 37′ 38″ W	11.6	35.2	0.9	38	Iceland Basin
DD11J	04/08/02	60° 21′ 10″ N 31° 00′ 26″ W	11.1	35.0	0.8	47.4	Reykjanes Ridge
B1J	31/07/02	61° 40′ 45″ N 27° 00′ 52″ W	10.9	35.0	1.0	33.3	Irminger Basin
B5J	02/08/02	63° 00′ 54″ N 29° 59′ 32″ W	10.2	34.9	0.5	56	Irminger Basin
C8J	10/08/02	63° 29′ 51″ N 36° 02′ 24″ W	9.9	35.0	1.2	67.4	Greenland shelfbreak

Fig. 2. Initial nano- and microplankton concentrations and composition at the different experimental stations. (A) Spring (B) summer

Frost (1972) for the taxa where there was a significant difference in concentration between controls and incubation bottles.

Food selection on specific phytoplankton groups was quantified using the selectivity index (SI) proposed by Chesson (1978). This index varies between 0 and 1 with SI_i = 0.5 indicating non-selective feeding towards the prey i, $SI_i > 0.5$ indicates a preference for the prey i and $SI_i < 0.5$ indicates discrimination against the prey i.

RESULTS

Food field

Given the wide spatial and temporal coverage of this study (Fig. 1), we carried out experiments for a wide range of naturally occurring food conditions (Fig. 2a,b). In spring, the composition of nano- and microplankton differed significantly between stations (Fig. 2a). The Greenland shelf was characterized by a *Phaeocystis* sp. bloom reaching up to 212 mg C m^{-3}. In the Irminger Basin ciliates of the *Strombidium* type (20 to 30) dominated the biomass. In the Reykjanes Ridge region, the biomass was distributed almost equally between *Strombidium* and diatoms (mainly *Chaetoceros pelagicus*). Finally, in the Iceland Basin, the nano- and microplanktonic community was more diverse, with significant biomass contributions from *Strombidium* sp., diatoms (*C. pelagicus*),
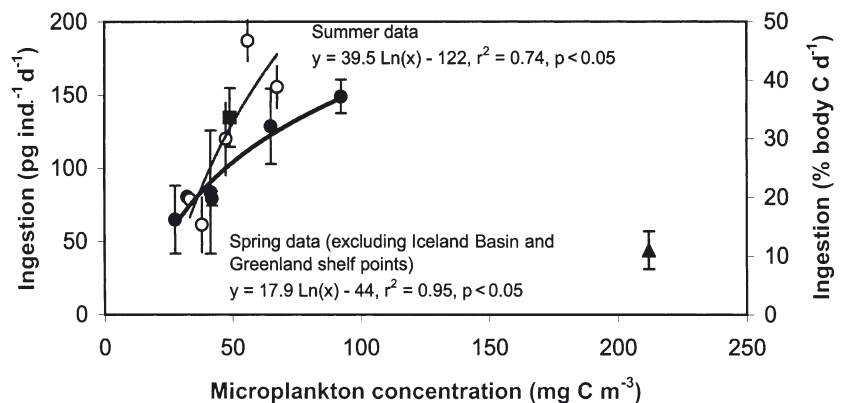
cubated on a plankton wheel (0.1 rpm) for ~24 h at sea surface temperature. A further bottle was filled and immediately fixed with acidic Lugol to estimate the food concentration at Time 0. Experiments were terminated by adding acidic Lugol to the bottles (1% final concentration, Holligan & Harbour 1977).

A subsample of 100 ml (½ the incubation volume) was settled (Utermöhl 1958) and counted under an inverted microscope following Båmstedt et al. (2000). Heterotrophic dinoflagellates were separated from autotrophic forms according to Lessard & Swift (1986) and Burkill et al. (1993). Phytoplankton carbon biomass was estimated from cell volume (Strathmann 1967) and using a factor of 0.21 pg C μm^{-3} (Ohman & Runge 1994) for ciliates. No correction was applied for ciliate losses and cell shrinkage. Filtration and ingestion rates were calculated from the carbon concentrations following

Fig. 3. Ingestion rates expressed as pg C ind.$^{-1}$ d^{-1} (left axis) and as % body C d^{-1} (right axis) as a function of nano- and microplankton carbon concentration. We assumed an average body weight of 0.4 µg C ind.$^{-1}$ in calculations (Turner et al. 2001). (●) Spring data; (○) summer data. (▲) Stn C6M (dominated by *Phaeocystis* sp. colonies), (■) Stn I1M (warmer Iceland Basin). Vertical bars: SE of the average for the ingestion expressed as pg C ind.$^{-1}$ d^{-1}

dinoflagellates (*Dinophysis acuminata*, *Gyrodinium britannicum*), and small flagellates (2 to 5 μm).

In summer, the biomass on the Greenland shelf was lower (67 mg C m^{-3}) and dominated by small flagellates. Small flagellates also dominated in the Irminger Basin. In the Reykjanes Ridge region, the main components were small flagellates and diatoms (*Tropodineis* sp.). Again, the biomass in the Iceland Basin was distributed between diatoms *Tropodineis* sp., dinoflagel-

lates *Ceratium tripos*, *Protoperidinium depressum*, small flagellates and ciliates *Strombidium* sp. (Fig. 2b).

Feeding

Ingestion ranged from 0.044 to 0.135 μg C ind.$^{-1}$ d^{-1} in spring, and from 0.062 to 0.187 μg C ind.$^{-1}$ d^{-1} in summer (Fig. 3). Feeding rates were generally related
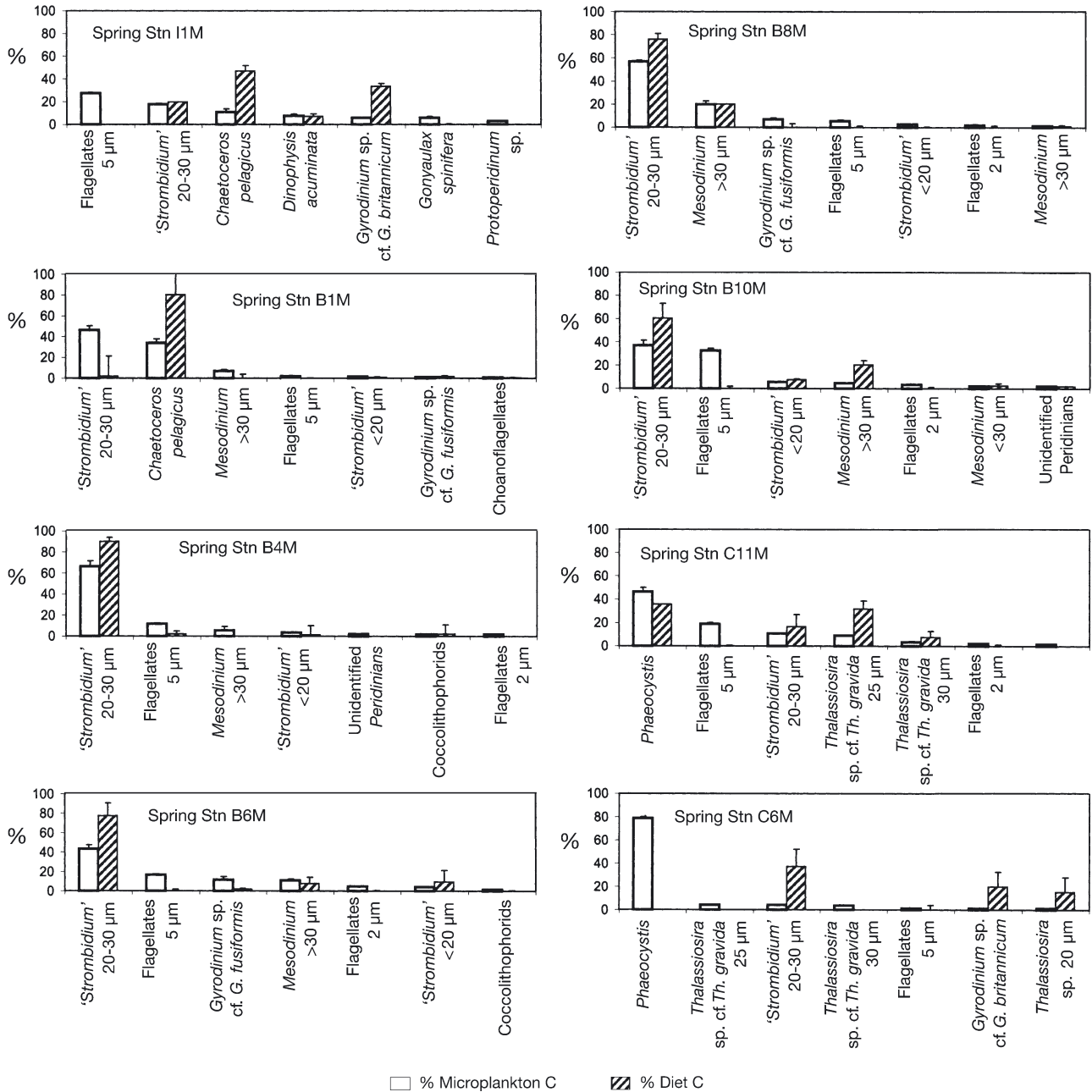

Fig. 4. (Above and next page) Percentage contribution of different types of cells to the nano- and microplankton and to the diet of *Calanus finmarchicus* nauplii at the different stations. Vertical bars: SE of the average
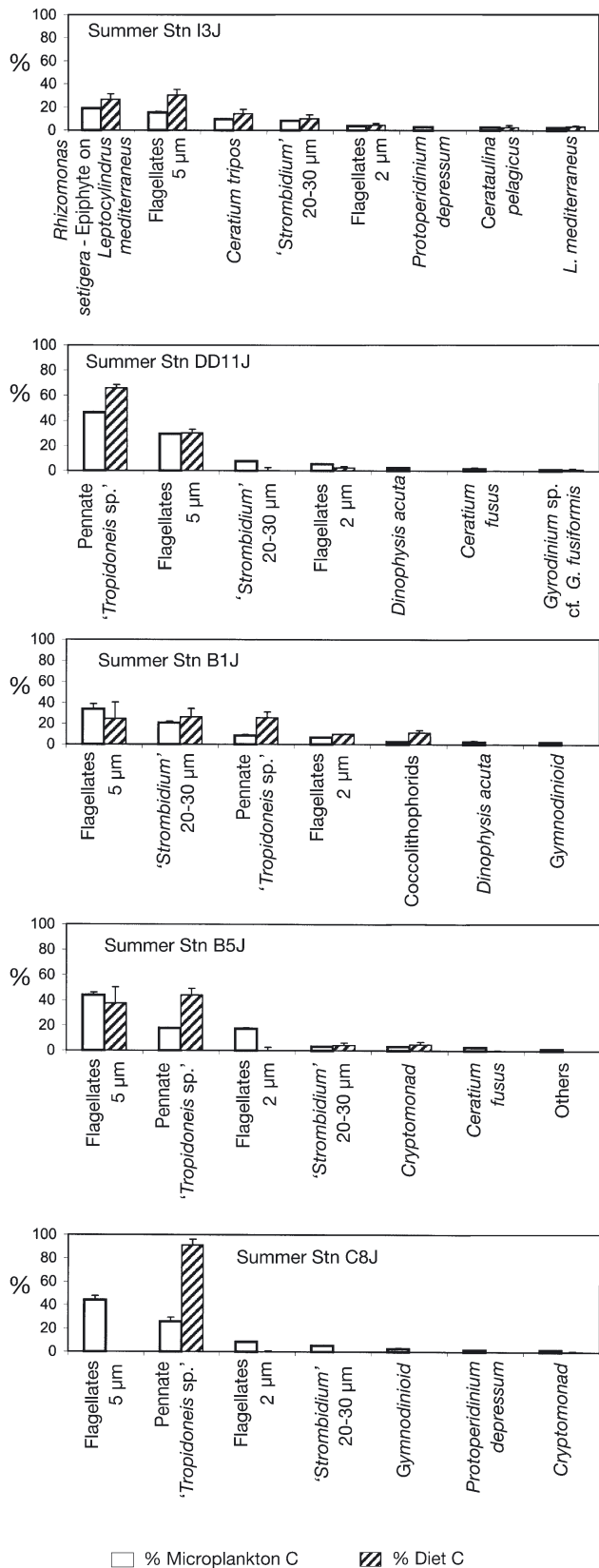
Fig. 4. (continued)

to the food concentration, except for the experiment with the *Phaeocystis* sp. bloom water (Stn C6M, Fig. 3). In the latter experiment, ingestion rates were much lower than that expected from the general relation between ingestion and food concentration (Fig. 3).

Interestingly, at Stn I3 in summer, a large fraction of the biomass was due to an epiphyte *Rhizomonas setigera* on the diatom *Leptocylindrus mediterraneus*. Although this epiphyte was important in the diet (Fig. 4), its capture has to be associated with that of the diatom.

Clearance rates and selectivity

The *Calanus finmarchicus* nauplii showed size selection, with no detectable ingestion of small flagellates during the spring cruise and lower ingestion rates than expected from their relative contribution to the ambient nano- and microplankton in summer. Although clearance rates on them were lower than those on large cells (Table 2), during the summer 5 µm flagellates contributed significantly to the diet (Fig. 4).

There were also clear differences between the feeding rates on larger cells (Table 2). *Phaeocystis* colonies were not ingested in spring at Stns C6M and C11M on the Greenland shelf (Fig. 4). *Strombidium* sp was actively selected at the Irminger Basin Stns B4M, B6M, B8M and B10M (Fig. 4). However, when the percentage of diatoms was higher (Stns I1M and B1M) they were cleared at higher rates than ciliates and other small cells. This was the case both in spring and summer, when diatom composition was dominated by *Calanus pelagicus* (Stns I1M and B1M) and *Tropodineis* sp. (Stns I3J and DD11J), respectively. In fact, selectivity on *Strombidium* sp. decreased with increasing percentage diatom concentration (Fig. 5a) and this was due to a decrease in the filtration rate on *Strombidium* sp. (Fig. 5b).

DISCUSSION

The maximum clearance rates on large cells measured here are similar to rates from other field (Turner et al. 2001) and laboratory (Paffenhöfer 1971) studies. When measurable, clearance rates on small cells were also similar to laboratory measurements (Rey et al. 2001, Meyer-Harms et al. 2002). Apparently, *Calanus finmarchicus* nauplii feed comparatively inefficiently on small cells and clearance rates increase with cell size (Fernandez 1979, Rey et al. 2001, Meyer-Harms et al. 2002).

The inefficient feeding on small cells effectively explains why the recruitment of *Calanus finmarchicus* nauplii to copepodites is linked with phytoplankton

Table 2. Maximum naupliar filtration rates on different types of cells

Cruise Species	Maximum filtration rate (ml ind.$^{-1}$ d^{-1})	Stn
Spring		
Chaetoceros socialis	20.3	C6M
Guinardia striata (*Rhizosolenia stolterfothii*)	15.3	B6M
Thalassiosira sp. (cf. *Th. gravida* 25 µm)	12.6	C11M
Gyrodinium sp. (cf. *G. britannicum*)	11.7	I1M
Strombidium sp. (>30 µm)	11.7	B1M
Mesodinium sp. (>30 µm)	10.1	B10M
Chaetoceros pelagicus	10.0	I1M
Strombidium sp. (20–30 µm)	7.6	B6
Summer		
Cocolithophorids	27.1	B1J
Nanoneis haslea	14.4	B5J
Tropidoneis sp.	13.4	C8J
Gyrodinium sp. (cf. *G. fusiformis*)	12.0	C8J
Flagellates 5 µm	4.2	DD11J
Flagellates 2 µm	1.8	DD11J

blooms. Small flagellates suffer heavy predation from other microzooplankton (Gifford et al. 1995) and do not usually reach sufficient concentrations to effectively sustain a *Calanus* nauplius with a clearance rate of <5 ml ind.$^{-1}$ d^{-1} (Table 2). When the concentration of larger cells increases at the onset of the bloom, the higher filtration rates on diatoms (>10 ml ind.$^{-1}$ d^{-1}) may result in a disproportionate increase in ingestion rates. Campbell et al. (2001) found that a 70 mg C m^{-3} concentration was necessary for *C. finmarchicus* nauplii to achieve maximum growth rates. The differences in feeding efficiency we found indicate that whether maximum growth rates are attained in the field depends both on concentration and composition of the phytoplankton. This might also explain why during the summer in the North Atlantic, when phytoplankton biomass is still relatively high (~1 mg chl *a* m^{-3}) but dominated by small flagellates, there is no recruitment of additional cohorts of *C. finmarchicus* (Heath et al. 2000).

Calanus finmarchicus nauplii also clear ciliates at high rates, and ciliates make a significant contribution to the diet in areas with low phytoplankton biomass (Fig. 4). It has to be taken into account that in the present study, we did not correct for possible losses or shrinkage of ciliates, so their contribution to the diet is probably higher (Gif-

ford & Caron 2000). However, in the North Atlantic oceanic waters, ciliates rarely reach concentrations comparable to those of phytoplankton blooms (Gifford et al. 1995, Irigoien et al. 1998), and it is therefore unlikely that ciliates can sustain the cohort's recruitment from nauplii to copepodite. It is probable that the increase in ciliate biomass in the North Atlantic oceanic waters follows the phytoplankton bloom because the latter is the major input of organic matter into the system (Irigoien et al. 1998).

Calanus finmarchicus seemingly ingests non-motile diatoms over motile ciliates, contrary to what has been proposed to be the adult behaviour (e.g. Nejstgaard et al. 2001). Different phytoplankton may have different nutritional values affecting survival and growth of *Calanus* nauplii (Huntley et al. 1987, Rey et al. 2001). *Calanus* nauplii are able to select between particles
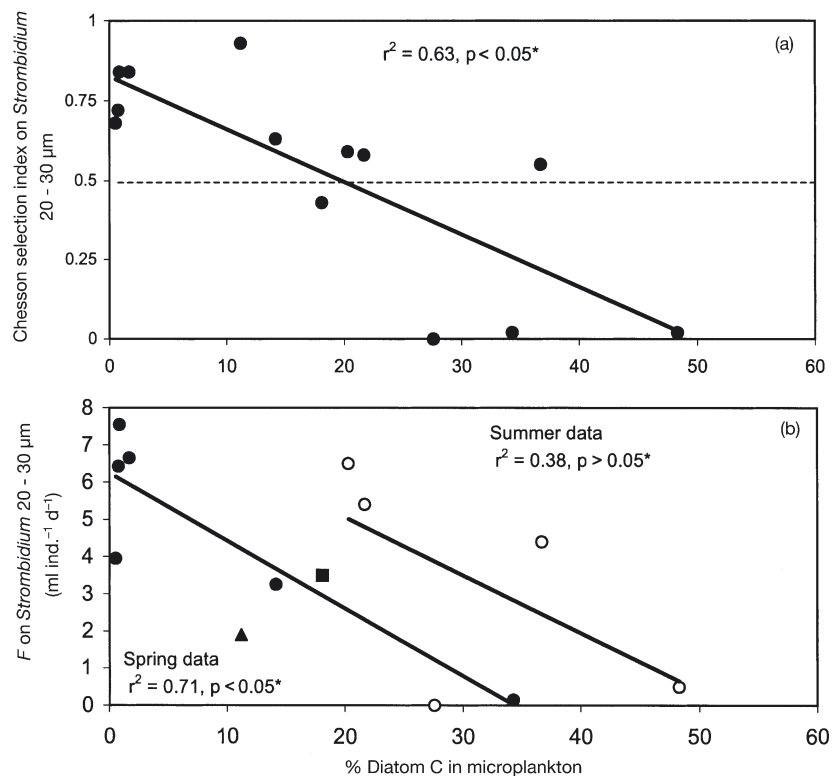

Fig. 5. (a) Chesson's selection index on *Strombidium* sp. (20 to 30 µm) vs percentage of diatoms in the microplankton. *Untransformed data presented but r^2 and p calculated after arcsine transformation of the data. (b) Filtration rates (F) on *Strombidium* sp. (20 to 30 µm) vs percentage of diatoms in the microplankton. Symbols as in Fig. 3. *Untransformed data presented but r^2 and p calculated after arcsine transformation of the data

of different quality (Fernandez 1979); however, a simpler explanation is also available. Many ciliates (and dinoflagellates) are able to detect fluid disturbances generated by moving or filtering predators, and respond to feeding currents by vigorous escape jumps (Jakobsen 2001, 2002). Consequently, the capture efficiency would be lower for ciliates than diatoms. When also considering the potentially long handling time for large chain-forming or pennate diatoms, the lower clearance rates on ciliates when diatoms are abundant are not surprising. Both the apparent preference for non-motile diatoms in our experiments, and the feeding rates, generally agree with the behavioural observations and model predictions of Titelman & Kiørboe (2003). Late naupliar stages of *Calanus* swim with a more or less continuous cruising motion, which allows for sufficient encounters with non-motile food, such as diatoms (Titelman & Kiørboe 2003). In contrast, nauplii with a jump-sink behaviour rely on prey motility for food encounter (Titelman & Kiørboe 2003).

The concept that adult *Calanus finmarchicus* prefer ciliates to phytoplankton also needs to be viewed with caution. For example, Irigoien et al. (1998) concluded that clearance rates of adult *C. finmarchicus* on ciliates are higher than on phytoplankton, but their observations related ingestion to total phytoplankton with a high percentage of small cells. When relating ingestion to chl *a* > 5 µm, clearance rates on phytoplankton were at least as high as those on ciliates. It is also important to distinguish between pre- or post-bloom and bloom periods when diatoms dominate. Often cited as examples of *Calanus* preferring ciliates, Fessenden & Cowles (1994) and Levinsen et al. (2000) actually showed that ciliates are important before or after the bloom, but when the diatom bloom develops their contribution to diet becomes negligible. This may suggest a general sequence of food preference for *Calanus*; diatoms > ciliates > small phytoplankton. However, our data (Table 2) indicates that such a clear distinction between microplanktonic food categories does not really exist (e.g. high filtration rates on *Gyrodinium britannicum*).

Food preference depends on a host of prey characteristics (size, behaviour, form, palatability etc.), predator characteristics (behaviour, hunger, nutritional requirements etc.) and environmental varialbes (turbulence, temperature). It is not possible to include such complexity in models of the copepod population dynamics in the North Atlantic (e.g. Heath et al. 2000). Nevertheless, our results indicate that at least 2 factors should be regularly measured in the field and considered in models, if they are to correctly predict the recruitment of *Calanus* copepodites: the concentration of ciliates and the concentration of chl *a* > 5 µm.

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