The relative importance of protozooplankton and copepods as grazers on phytoplankton during the 1999 spring bloom on the Faroe Shelf

Lutfalsliga ávirkanin av protozooplankton og kopepodum á várblóming av plantuplankton á landgrunninum í 1999

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Úrtak

Kanningarnar vórðu gjørdar undan várblómingini og í várblómingini. Í tíðarskeiðinum undan várblómingini var lítið til av plantuplankton (< 3 mgC m^{-3} í miðal), men í várblómingini vóru nøgdirnar í miðal 201 mg Cm^{-3}. Nøgdirnar av protozooplankton vóru sum heild lágar, men vístu somu gongd sum plantuplankton. Tann stóri kopepodurin *Calanus finmarchicus* myndaði í stóran mun nøgdirnar av djóraplankton alt tíðarskeiðið. Av teimum smærri kopepodunum var *Pseudocalanus* spp. at finna í lutfalsliga stórum nøgdum í tíðarskeiðinum undan várblómingini, meðan *Acartia longiremis* og *Temora longicornis* vóru at finna í størri nøgdum undir várblómingini. Orsakað av gýtingini hjá djóraplankton sæst ein broyting frá samansetingini av djóraplankton frá vaksnum kopepodum undan várblómingini til smærri kopepodittar í várblómingini. Ávirkanin av protozooplankton á plantuplankton varð mett til at vera sera lítil alt tíðarskeiðið. Hinvegin, varð mett, at møguleiki var fyri stórari ávirkan frá kopepodum á plantuplankton í tíðarskeiðinum undan várblómingini.

Abstract

The research period was split up in two different productive periods: a pre-bloom and a mid-bloom separated by a transition period of 2 weeks. In the pre-bloom period the biomass of phytoplankton was low (< 3 mgC m^{-3} on average), but during mid-bloom the biomass was 201 mgC m^{-3} on average. The protozooplankton biomass was only slightly higher during mid-bloom (3.5 mgC m^{-3}) than during pre-bloom (1.4 mgC m^{-3}). The large oceanic copepod *Calanus finmarchicus* dominated the copepod biomass with more than ¾ during both periods. *Pseudocalanus* spp. dominated small neritic copepods during pre-bloom while *Acartia longiremis* and *Temora longicornis* were more numerous during mid-bloom. As a result of spawning success a clear shift in development stage composition towards younger stages was observed from pre- to mid-bloom. The estimated grazing impact on the phytoplankton by the protozooplankton and the copepods was negligible during mid-bloom. However, during pre-bloom the copepod grazing impact on the phytoplankton standing stock was potentially high. Our results suggested that grazing by the protozooplankton during pre-bloom was negligible.

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Introduction.

The structure of the grazer community during spring bloom situations in temperate and arctic waters has been intensively studied in the past. Most attention has been paid to the mesozooplankton, especially the copepods. However, two decades ago it became evident that protozoa potentially play an important role in the linkage between primary production and higher trophic levels (e.g. Smetacek, 1981; Azam *et al.*, 1983; Fenchel, 1988). More effort has therefore been allocated in research concerning the protozooplankton community and its role in carbon flow (Hansen, 1991; Nielsen *et al.*, 1993; Ohman and Runge, 1994; Nielsen and Hansen, 1995; Levinsen *et al.*, 1999; Jensen and Hansen, 2000).

The Faroe Shelf is basically a neritic ecosystem relatively isolated from its oceanic surroundings by a persistent tidal front surrounding the islands at about 100-130m bottom depth contour (Hansen, 1992a). There is an anticyclonic circulation of these shelf water masses, and the average residence time has been estimated to be about 3 months (Gaard and Hansen, 2000). Because of very strong tidal currents the water column in the shallow parts of the shelf is well mixed during summer, usually without any stratification. Theoretically, sufficient light conditions for spring bloom development therefore are when the critical depth has exceeded the bottom depth in this region.

Due to these hydrographic conditions the Faroe Shelf hosts a unique phytoplankton (Gaard, 1994; 1996a; Gaard *et al.*, 1998) and mesozooplankton (Gaard, 1994; 1996b; 1999) composition compared to the oceanic surroundings. Although fairly isolated the Faroe Shelf is, however, also affected by the surrounding oceanic environment, including import of *Calanus finmarchicus*. Once on the shelf, this large copepod seems to have a great influence on the shelf ecosystem. This oceanic influence is, however, highly variable, and the amount of *C. finmarchicus* that are advected onto the shelf, varies very much between years (Gaard, 1999; 2000; Gaard and Hansen, 2000).

The importance of the protozooplankton as phytoplankton grazers on the Faroe Shelf ecosystem is still not investigated despite the recent years acknowledgment of its importance for grazing and carbon flow elsewhere (e.g. Paranjape, 1987; 1990; Levinsen *et al.*, 1999).

The objective of this work was:

1. to study the structure of the grazer community on the Faroe Shelf during two different periods in the spring-summer succession: a low productive pre-bloom period, and a high productive mid-bloom period.
2. to investigate the relative importance of copepods and protozooplankton as grazers on the phytoplankton standing stock during these two periods.

Materials and methods

This investigation was carried out on the Faroe Shelf. Seawater temperature was monitored at a permanent station (station S in Fig. 1), while biological measurements were carried out at station H north-

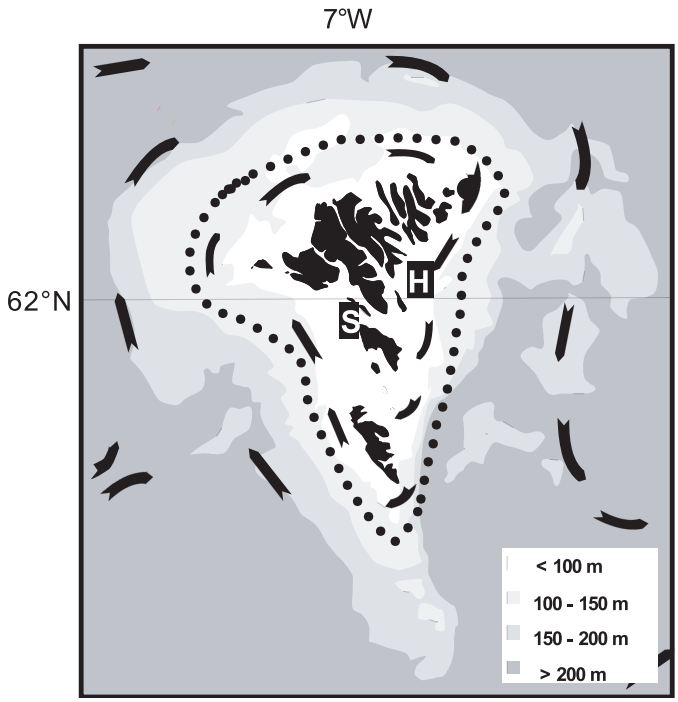

Figure 1. Topography and main features of the flow field around the Faroes. The two black dots with letters beside them refer to sampling stations. The broken line enclosing the light gray area around the shelf indicates the typical position of the tidal front that separates the shelf water from the open ocean.

east of Tórshavn (54 m bottom depth) during a spring-bloom situation in 1999 (Fig. 1). Samples were taken on 13 cruises from 19 April until 21 June. On each cruise samples were taken for chlorophyll *a* measurements, abundance and species composition of phytoplankton, copepods and protozooplankton, and egg production by *C. finmarchicus* was obtained.

Water samples for chl *a*, phytoplankton and protozooplankton species identification were taken with 5 L Niskin bottles at 2 and 20 m depth and preserved with Lugol's (final conc. 1%).

For measurements of chl *a*, duplicates (2 × 2 L) of seawater were filtered through a Watman GF/C filter, and chl *a* concentration measured according to the method described by Baltic Marine Biologists (1979) with the modification that homogenization was carried out using a Soniprep 140 ultrasound homogenizer. Chl *a* concentrations were calculated according to the equation of Jeffrey and Humprey (1975).

The phytoplankton samples were counted and identified in 2, 5 or 10 mL subsamples after overnight settlement, using an inverted microscope. Cell size of approximately 10 cells from each species/genus was measured and converted to biomass (cell carbon) using the equation for diatoms from Menden-Deuer and Lessard (2000) and the regression model for nanophytoplankton from Verity *et al.* (1992). Protozooplankton (> 10μm) was counted and identified in 50 mL subsamples after overnight settlement, using an inverted microscope. Because of low cell concentra-

tion all cells in the subsample were counted (on average 25-30 ciliates and 35-40 dinoflagellates). Each cell was measured and converted to biomass (cell carbon) using the equation for dinoflagellates and aloricate ciliates from Menden-Deuer and Lessard (2000).

The ingestion rate of the protozooplankton community during pre-bloom was calculated assuming that total loss rate was due to copepod grazing and no prey selection by the copepods. The ingestion rate of the protozooplankton during this period is thus estimated from the calculated copepod ingestion rate during pre-bloom (using both copepod egg production and the temperature dependent production method from Huntley and Lopez (1992)). During mid-bloom the growth rate constant μ of the thecate heterotrophic dinoflagellates was calculated using the increase in biomass during mid-bloom: $\mu = [\ln(B_t/B_0)]/t$, where B_o = biomass at the beginning of the period, B_1 = biomass at the end, and t = length of the time interval (days). Ingestion was calculated using a gross growth efficiency of 40% (Hansen *et al.*, 1997).
Copepods were sampled in vertical hauls from 50 m depth to the surface using a 200 μm mesh size WP-2 net. The volume filtered was measured with a Hydro Bios flow meter with back run stop attached to the net opening. A total of 3 replicate tows were taken on each cruise. Towing speed was 1/3-1/2 m s^{-1}. The samples were preserved in 4% buffered formaldehyde. In the laboratory, sub-samples of 300-400 animals were taken using a Motoda cylinder splitter, identified and counted. The cephalothorax length was measured on each copepod (total length for nauplii and non copepods), and biomass (μgC ind^{-1}) was calculated using length/weight regressions derived from the literature specified for each group: *Calanus finmarchicus* (Hirche and Mumm, 1992); *Pseudocalanus* spp., *Temora* spp. and *Centropages* spp. (Klein Breteler *et al.*, 1982); *Acartia* spp. (Berggreen *et al.*, 1988); *Microcalanus* spp. and *Oithona* spp. (Sabatini and Kiørboe, 1994).

For egg production measurements of *C. finmarchicus,* live females were collected using a 200 μm mesh size WP-2-net equipped with a 2 L non-filtering cod-end. Healthy females (n = 10-13) were incubated individually at *in situ* temperature and dim light in false bottom containers (mesh size 400 μm) containing approximately 1 L of 60 μm filtered seawater. Incubation period was 24 h. After incubation, the eggs were filtered through a 30 μm mesh net and counted. Female cephalotorax and the diameter of 5-10 eggs were measured. Female carbon content was calculated according to length-weight regressions from Hirche and Mumm (1992). Assuming a carbon: DW of 0.6, egg carbon was calculated using a volume to carbon conversion of 0.14×10^{-6} μgC μm^{-3} (Kiørboe *et al.*, 1985).

The ingestion rate of the copepod community was estimated according to egg production in *C. finmarchicus* females. Egg production was converted to biomass specific production rates (P/B), and ingestion rate was calculated for the entire copepod community using a gross growth

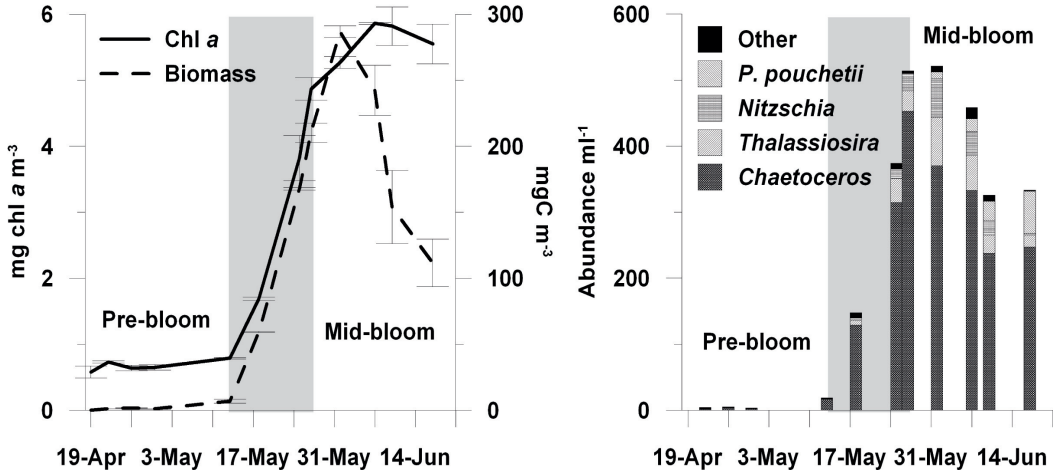

Figure 2. Left: Average chlorophyll a concentration (mg m^{-3}) 1'-axis, and phytoplankton biomass (mgC m^{-3}) 2' axis. Right: Phytoplankton abundance (ml^{-1}) and species composition. Vertical bars indicate standard error of the mean of the 2 m and 20 m depth samples (n = 2). The shaded area indicates the transition period between the pre-bloom and the mid-bloom.

efficiency of 33% (Peterson, 1988) assuming juvenile somatic growth is equal to the specific egg production rate (Berggreen *et al.*, 1988), and that all copepods followed the P/B for *C. finmarchicus*.

As a second estimate of copepod ingestion rate we used the temperature dependent production method from Huntley and Lopez (1992), where growth $G = 0.0445e^{0.111T}$, where T is the ambient temperature of the water column. The copepod ingestion was calculated as $I = 3 \times G \times B$, where B = the biomass of copepods and assuming a gross growth efficiency of 33% (Peterson, 1988).

Results

Hydrography and phytoplankton

The water column on the Faroe Shelf is well mixed with usually no summer stratification. The temperature measured at station S (Fig. 1) is thus considered to be representative for the temperature in the whole water column in the central part of the shelf. There was a steady rise in temperature throughout the investigation from 6.3°C on 19 April to 8.4°C in late June (data not shown).

The experimental period was divided into two different scenarios based on standing stock of phytoplankton: the pre-bloom and the mid-bloom period, with a transition period of 2 weeks. The chl *a* concentration started to increase in mid May, and reached a maximum in early June (Fig. 2, left). The chl *a* concentration at 2 and 20 m depth were almost identical as would be expected since the water column usually is well mixed. The standard error in Fig 2 is taken between the mean chl *a* concentration (duplicates) at the two depths, n = 4 per date. The phytoplank-

ton species composition was totally dominated by diatoms. Especially *Chaetoceros* spp. were abundant (Fig. 2, right). The gelatinous colonial haptophyte *Phaeocystis pouchetii* first appeared at the start of the bloom, and increased much in abundance towards the end of the research period.

Protozooplankton

The protozooplankton community consisted of ciliates and heterotrophic dinoflagellates. The ciliate community was totally dominated by the genus *Strombidium*, while the heterotrophic dinoflagellates mainly consisted of the naked *Gyrodinium* spp. and the thecate *Protoperidinium* spp. The abundance and biomass of ciliates was low throughout the whole investigation, and showed no response to the increase in phytoplankton biomass from the pre-bloom to mid-bloom (Fig. 3 A and B). The number of heterotrophic thecate dinoflagellates was low during pre-bloom but increased with a slight time lag compared to the phytoplankton biomass (Fig. 3 C). This pattern is also reflected in the biomass, which starts to increase shortly after the initiation of the spring bloom (Fig. 3 D).

There was no clear response in abundance and biomass of naked heterotrophic dinoflagellates to the increased phytoplankton biomass during the shift from pre-bloom to mid-bloom.

The ingestion rate of the protozooplankton community during pre-bloom was calculated assuming that total loss rate was due to copepod grazing and no prey selection by the copepods. Using these assumptions and the *Calanus finmarchicus* egg production measurements for calculations of the copepod grazing pressure on the protozooplankton, yielded a growth rate of 0.08 d^{-1} for the entire protozooplankton community during pre-bloom.

During mid-bloom only the thecate heterotrophic dinoflagellates showed a response to the increased phytoplankton standing stock. This response in the period from 27 May until 17 June was used to calculate a growth rate constant of 0.15 d^{-1} for the thecate heterotrophic dinoflagellates.

The ciliates and the naked heterotrophic dinoflagellates showed no response to the increased phytoplankton standing stock.

Copepods

During pre-bloom the copepod community consisted mainly of the neritic copepods *Pseudocalanus* spp., *Acartia longiremis* and *Temora longicornis* and the large oceanic copepod *Calanus finmarchicus* (Fig. 4A). In terms of biomass, it was totally dominated by *C. finmarchicus* (Fig. 4B), which during this period constituted on average 81% of the total copepod biomass. The category "other copepods" in Fig. 4A includes *Microcalanus* sp., *Centropages typicus*, *Oithona similis* and unidentified copepods, mainly small stages of different neritic copepods.

As the spring bloom progressed the copepods increased in abundance reaching a peak in early June, slightly after the maximum in chl *a* concentration. This rise in number of copepods is mainly due to a rise in young stages i.e. nauplii and CI-

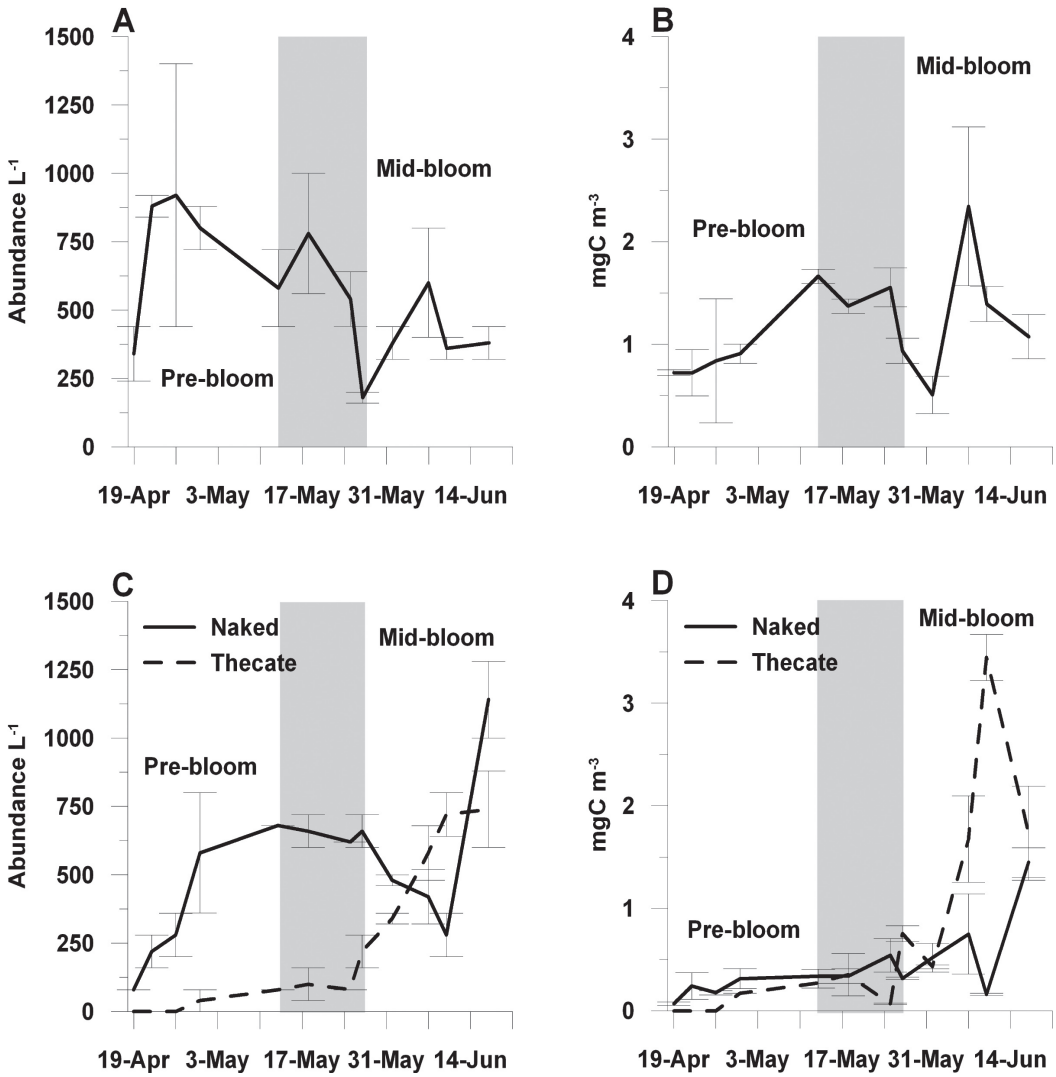

Figure 3. Average abundance (L^{-1}) and biomass (mgC m^{-3}) of ciliates (A and B) and heterotrophic dinoflagellates (C and D). Vertical bars indicate standard error of the mean of the 2 m and 20 m depth samples (n = 2). The shaded area indicates the transition period between the pre-bloom and the mid-bloom.

CIII of *C. finmarchicus* (Fig. 4C), which during this period constituted on average 80% of the total *C. finmarchicus*, and up to 50% of the total copepod community (by numbers). The biomass was also dominated by *C. finmarchicus* during mid-bloom with 77% of the total copepod biomass. At the end of the research period the smaller

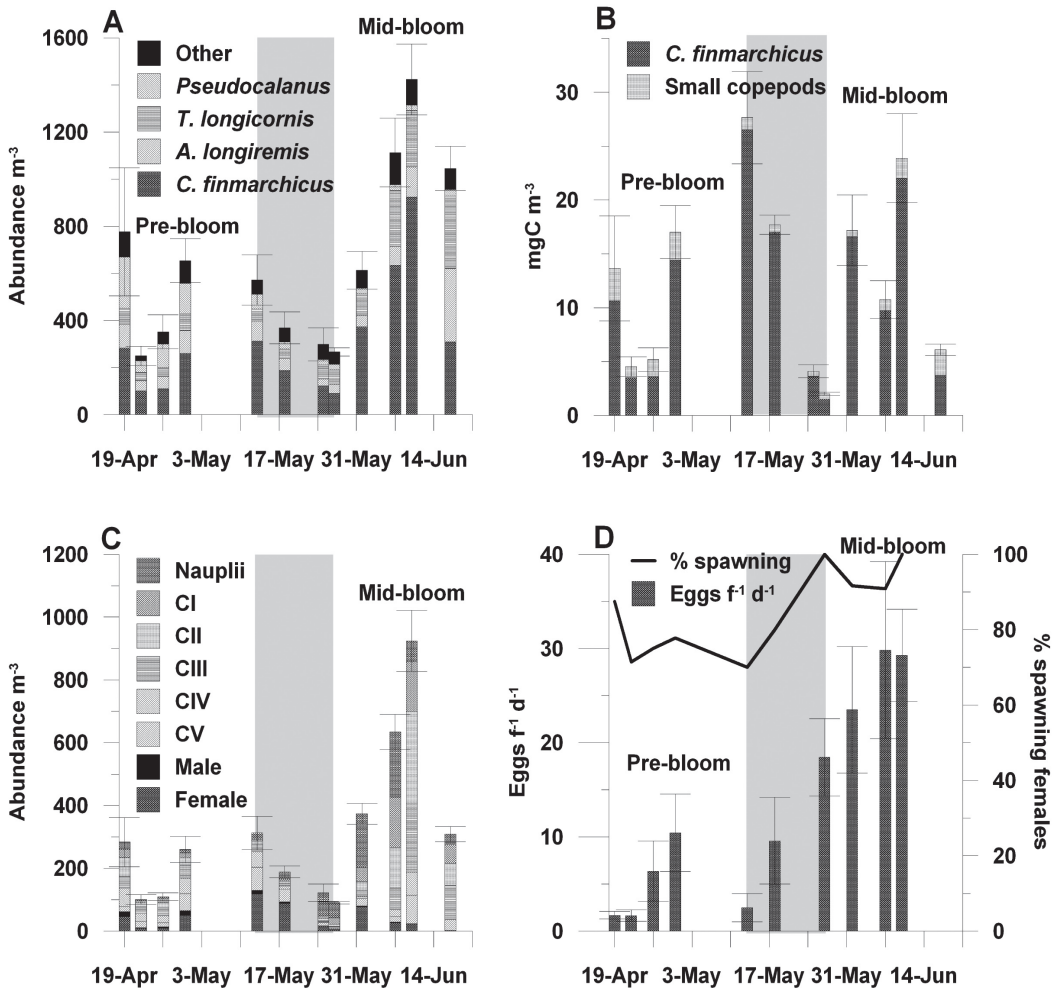

Figure 4. A and B: Average abundance (m^{-3}), species composition and biomass (mgC m^{-3}) of the copepod community. C: Average abundance (m^{-3}) and developmental stage composition of Calanus finmarchicus. Vertical bars indicate standard error of the mean of three vertical hauls from 50 m depth to the surface at each cruise. D: Average egg production of Calanus finmarchicus females (bars) and % spawning females (line) during the study period.

The shaded area indicates the transition period between the pre-bloom and the mid-bloom.

copepods (mainly *T. longicornis* and *A. longiremis*) increased in numbers while *C. finmarchicus* (especially the older stages CIV-adults) decreased. This change in the copepod species composition is clearly reflected in the biomass, which shows a distinct reduction towards the end of the research period (Fig. 4B).

	Egg production		
	Eggs × f^{-1} × d^{-1}	*n*	*Eggs* × m^{-2} × d^{-1}
Pre-bloom	4.5 ± 1.9	42	9781 ± 4799
Mid-bloom	25 ± 6.2	47	42108 ± 18156

Table I. Average egg production ± SE (standard error of the mean) of Calanus finmarchicus during pre- and mid-bloom; n = number of replicates during the period.

Egg production

Fecundity of *Calanus finmarchicus* followed the pattern of chl *a* concentration (Fig. 4D). During pre-bloom it was low with an average of 4.5 eggs female^{-1} d^{-1}, corresponding to an average of 9781 eggs m^{-2} d^{-1} (Table 1). In late May, the egg production increased, reaching an average of 25 eggs female^{-1} d^{-1}, corresponding to 42108 eggs m^{-2} d^{-1} during mid-bloom. On the last two sampling dates the abundance of healthy *C. finmarchicus* females was too low for egg production measurements.

The percentage of spawning females increased during the investigation period from 75% during pre-bloom to more than 95% during mid-bloom (Fig. 4D).

Discussion

Response of protozooplankton and copepods to the spring bloom

The thecate heterotrophic dinoflagellates showed a clear response to the increase in phytoplankton standing stock from pre- to mid-bloom. *Protoperidinium* spp. first appeared during the transition period and increased in numbers during the rest of the investigation. This response in thecate heterotrophic dinoflagellates is consistent with other results from coastal areas showing a dominance of thecate dinoflagellates in association with diatom blooms (Jacobson, 1987; Lessard 1991). The naked heterotrophic dinoflagellates *Gyrodinium* spp. on the other hand, did not show any biomass response to the increased phytoplankton biomass. This is in contrast to other investigations where the abundance of this species was closely related to the phytoplankton spring bloom (Hansen, 1991; Smetacek, 1981). One possible reason for a lack of response in the naked heterotrophic dinoflagellates could be due to the nature of their feeding mechanism. Naked heterotrophic dinoflagellates usually ingest intact prey of their own size by direct engulfment (Hansen and Calado, 1999); a phytoplankton bloom totally dominated by large spiny *Chaetoceros* species would therefore not seem to be their ideal prey item. Thecate dinoflagellates of the genus *Protoperidinium*, on the other hand, usually ingest their prey with a pseudopodium that extends through the flagellar pore and envelopes the prey (Jacobson and Anderson, 1986; Gaines and Elbrächter, 1987; Hansen and Calado, 1999). This feeding mechanism makes it possible for them to ingest relatively large prey organisms, like

chain forming diatoms, hence also *Chaetoceros* spp.

The ciliate community did not respond to the phytoplankton bloom. Like in the case of the naked heterotrophic dinoflagellates, the lack of response could be attributed to their feeding mechanism. A prey/predator relationship of approximately 1:10 in cell diameter has been shown for ciliates (Fenchel, 1986; Jonsson, 1986; Hansen *et al.*, 1994), which renders a diatom bloom dominated by large chain forming species of little value for most ciliates.

The copepod community showed a clear response to the phytoplankton bloom, peaking in abundance shortly after the chl *a* maximum in early June. The species composition was consistent with previous investigation on the Faroe Shelf (Gaard, 1999) with the presence of key species like *Pseudocalanus* spp., *Acartia longiremis*, *Temora longicornis* and *Calanus finmarchicus*. Of these, *C. finmarchicus* made up the bulk of the zooplankton biomass during both pre- and mid-bloom. However, the advection of this oceanic species onto the shelf is highly variable between years (Gaard and Hansen, 2000), but once on the shelf, it has a great influence on the shelf ecosystem (Gaard and Steingrund, 2001). The response to the bloom is also seen in the development stage composition of *C. finmarchicus*, which shows a distinct shift towards younger stages (nauplii-CIII) during mid-bloom (Fig. 4C).

However, using a WP-2 net with a mesh size of 200 µm will not sample small copepod species like *Oithona similis* and nauplii and small copepodite stages of most larger copepod species representatively. Even the smallest stages of the large copepod like *C. finmarchicus* will not be sampled quantitatively using this course mesh size (Nicols and Thompson, 1991; Munk *et al.*, 2003)

Grazing and carbon flow

In calculating the copepod community grazing impact on the phytoplankton standing stock, we have to consider protozooplankton as a potential food resource. In the past years it has been shown that especially during periods of low production, protozooplankton may be an important food resource for copepods (e.g. Ohman and Runge, 1994; Levinsen *et al.*, 2000). The abundance, and thus the importance of protozooplankton as food for the copepods, varied over the study period. During pre-bloom the biomass of protozooplankton made up more than 40% of the phytoplankton biomass. However, as the spring bloom started to develop the protozooplankton biomass likely became less important as it was diluted by the two orders of magnitude higher phytoplankton biomass.

Pre-bloom

As mentioned above the biomass of protozooplankton was about half of the phytoplankton biomass during pre-bloom. Assuming no prey selection by the copepods, the protozooplankton must have made up a substantial part of their diet during this period. This was taking into account when calculating the copepod grazing impact on the phytoplankton standing stock.

Based on *C. finmarchicus* egg production the average ingestion rate of the copepods was 0.4 mgC m^{-3} d^{-1} during pre-bloom (Table 2 and Fig. 5A) corresponding to 13% of the phytoplankton standing stock. Here we have made the assumption that juvenile somatic growth is equal to the *C. finmarchicus* specific egg production rate, and that all copepods follow the P/B for *C. finmarchicus*. This does, however, probably result in an underestimation of the total copepod ingestion since several recent studies have indicated that smaller copepods may often play a more important role than the larger animals, not only in terms of abundance but also in terms of biomass and grazing pressure on the phytoplankton (e.g. Morales *et al.*, 1991; Dam and Peterson, 1993). Calculating the ingestion rates per *C. finmarchicus* female gives an average ingestion rate of 2531 ngC f^{-1} d^{-1} during pre-bloom. Comparing this result with the pre-bloom ingestion rate of *C. finmarchicus* females (1433 ngC f^{-1} d^{-1}) at the weather station M (Mike) in the middle of the Norwegian Sea (Irigoien *et al.*, 1998) shows a slightly higher ingestion rate during our pre-bloom situation. Our results are calculated using the egg production results and length-weight regressions for weight of the females and eggs. The results in Irigoien *et al.* (1998) are pure herbivory based gut-fluorescence measurements without correction for possible pigment destruction. Their results are thus possibly slightly underestimated. The degree of pigment destruction during gut passage in copepods varies greatly but is generally believed to be <20% (Harris, 1996). Taking this into account our ingestion rates based on pre-bloom *C. finmarchicus* egg production seem to be in the same range as the ingestion rates measured at station M.

Application of the temperature dependent production method from Huntley and Lopez (1992) to our data gives an average ingestion rate of 1.0 mgC m^{-3} d^{-1} during pre-bloom (Table 2 and Fig. 5B), which corresponds to 37% of the phytoplankton standing stock. This gives an unrealistically high ingestion rate of 8443 ngC f^{-1} d^{-1} per female.

To estimate the growth rate of the whole protozooplankton community during pre-bloom we used the estimated copepod ingestion rates from both the egg-production and from the temperature dependent production method. In addition we assumed that the entire loss rate of the whole protozooplankton community during this period was due to copepod grazing, and no prey selectivity by the copepod community. This yields protozooplankton growth rates of 0.08 d^{-1} and 0.28 d^{-1}, for the egg-production and the temperature dependent production method, respectively. The latter of these two is unrealistically high, and using a gross growth efficiency of 40% (Hansen *et al.*, 1997) yields an estimated ingestion rate of 1.0 mgC m^{-3} d^{-1}, and a grazing impact of 37% on the phytoplankton standing stock. Based on egg-production the estimated ingestion rate of protozooplankton was 0.3 mgC m^{-3} d^{-1}, corresponding to 10% of the phytoplankton standing stock during pre-bloom.

However, the protozooplankton growth

rate of 0.08 d^{-1} is based on a relatively high estimated ingestion rate from the copepod community during pre-bloom. This high estimated ingestion rate from the copepod community, can be interpreted in two different ways:

1. The first possibility is that primary production during pre-bloom actually could have been high during this period, but due to grazing a build up of biomass was prevented.
2. The second possibility is that the copepod community during pre-bloom partly relies on lipid reserves to fuel gonad development and egg production.

There has been some speculation in the past years as to what extent copepods are able to control the onset of the phytoplankton spring bloom. Yin *et al*. (1997) reported on the importance of the large oceanic copepod *Neocalanus plumchrus* during early spring from the Strait of Georgia, British Columbia. A large biomass of this copepod prior to spring-bloom, was able to suppress and thus delay the spring bloom development. Bathmann *et al*. (1990) found a large influence of copepods on the spring-bloom development in the Norwegian Sea, and postulated that if the upward migration of overwintering copepods occurred shortly before or concomitant with the diatom spring bloom, bloom formation could be hindered. Other researchers have, however, stated the opposite, and concluded that the grazer community is not able to control or postpone a spring bloom (e.g. Smith *et al.*, 1985; Hirche *et al.*, 1991; Nielsen and Hansen, 1995). It is, however, not likely that the copepods were suppressing the phytoplankton spring bloom during our study. If the grazer community actually was suppressing the development of the phytoplankton spring bloom, we would have expected *C. finmarchicus* to graze at a maximum, and hence show a much higher egg production rate during this period.

The most likely possibility for the high estimated ingestion rates during pre-bloom is probably that the females may have used stored lipids to fuel parts of the egg production during this period. There has been some debate about the importance of lipid storages during low productive pre-bloom periods. It is generally accepted that gonadogenesis and development of early oocyte in many *Calanus* species is partly fuelled by stored energy during winter (e.g. Hirche, 1996 and references therein), but to what extent these lipid reserves actually are used for egg production in *C. finmarchicus* is not certain. This has been proposed for the closely related species *Calanus helgolandicus* (Gatten *et al.*, 1979; 1980), and Hirche (1996) suggested that overwintering *C. finmarchicus* females might invest their lipid storages in egg production, since they may not have undergone the reported drastic lipid losses solely for maturing from the CV copepodite stage. This is supported by investigations in the Faroe-Shetland Channel and northern North Sea (Richardson *et al.*, 1999), the Labrador Sea (Cabal *et al.*, 1997) and at station M in the Norwegian

	Ingestion			
	Copepod	*Copepod**	*Protozooplankton*	*Protozooplankton**
Pre-bloom	0.4 ± 0.16	1.0 ± 0.26	0.3 ± 0.05	1.0 ± 0.17
Mid-bloom	1.6 ± 0.42	1.2 ± 0.21	0.6 ± 0.09	0.6 ± 0.09

Table II. Average ingestion (mgC m^{-3} d^{-1}) ± SE (standard error of the mean), for copepods and protozooplankton during pre- and mid-bloom. * = based on the temperature dependent production method (Huntley and Lopez, 1992). Average protozooplankton ingestion rates during mid-bloom are calculated based on thecate heterotrophic dinoflagellates only (see Fig. 5).

Sea (Irigoien *et al.*, 1998), where stored lipid reserves may be used to fuel, or supplement reproduction in *C. finmarchicus*.

Thus, to use egg production as an estimate for copepod community ingestion during pre-bloom may be erroneous. At this time of the year the amount of immature females is relatively high leading to an underestimation of the actual ingestion rate, as only spawning females are assumed to be actively feeding. Using only active spawning females may therefore give a more reliable indication of the ingestion rate for the copepod community. Also considering that egg production during pre-bloom situations may partially be fueled by stored lipid reserves makes it complicated to interpret egg production results from these periods and may overestimate the actual grazing impact. The temperature dependent production method, on the other hand, takes only the ambient temperature and the actual copepod biomass into account. This approach yields a very high potential ingestion rate during pre-bloom in our research, which then again is not reflected in the copepod egg production. Using this method thus probably also overestimates the actual grazing impact of the grazer community during pre-bloom.

Another way to estimate ingestion rates for copepods is to measure clearance rates for copepods. Levinsen *et al.* (2000) measured clearance rates by adult females of several different copepods on chl *a*, dinoflagellates and ciliates in Disko Bay, West Greenland, and Young Sound, NE Greenland during a post-bloom situation. Their results using *C. finmarchicus* females gave clearance rates of 312, 465 and 200 ml $female^{-1}$ day^{-1} for phytoplankton, ciliates and dinoflagellates, respectively. Multiplying these clearance rates with the biomass per cubic meter of phytoplankton, ciliates and dinoflagellates and the amount of *C. finmarchicus* females per cubic meter, and using a Q_{10} of 2.8 for temperature correction (Hansen *et al.*, 1997), yields a female ingestion rate of 0.083 mgC m^{-3} d^{-1}. Correcting this to total copepod community ingestion yields an ingestion rate of 0.18 mgC m^{-3} d^{-1} on the Faroe Shelf during pre-bloom. This is probably a more realistic value, and leads to a protozooplankton growth rate of 0.06 d^{-1}, corresponding to a grazing impact of 4% and 7% on the phytoplankton standing stock, for the co-

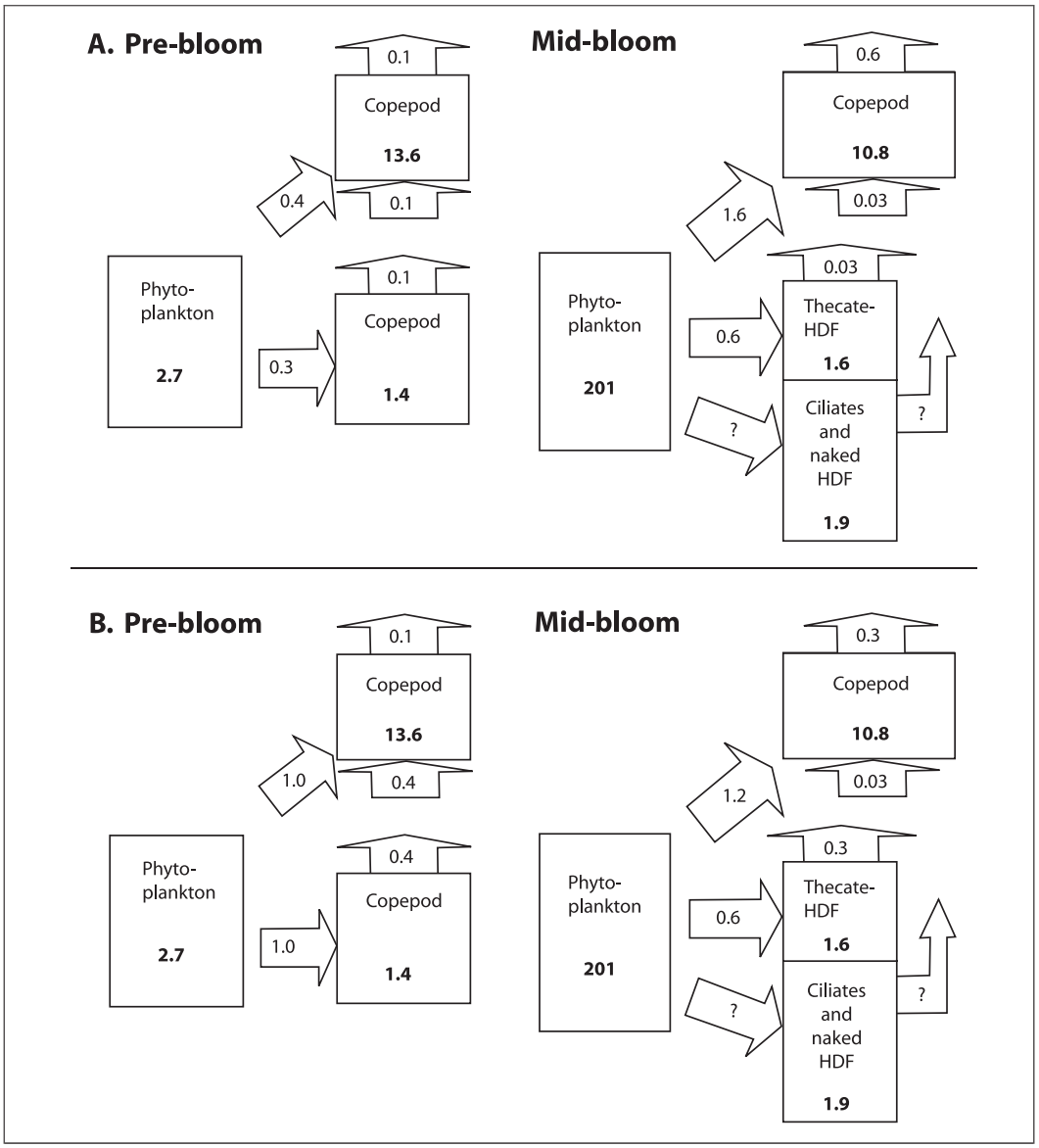

Figure 5. Carbon flow budgets based on measured biomass, and measured (egg production) or estimated (Huntley and Lopez 1992) production. A based on egg production, and B based on the temperature dependent production model for copepods only, from Huntley and Lopez (1992). Numbers in the boxes show average biomasses (mgC m^{-3}), and numbers in the arrows entering and leaving the boxes indicate consumption and production, respectively (mgC m^{-3} d^{-1}). HDF = heterotrophic dinoflagellates. The ingestion and production of the ciliates and naked HDF during mid-bloom are missing due to lack of biomass response to the increased phytoplankton standing stock.

pepod and protozooplankton community, respectively.

Mid-bloom

Based on *C. finmarchicus* egg production, the average ingestion rate for the copepod community during mid-bloom, was 1.6 mgC m^{-3} d^{-1} (Table 2 and Fig. 5A). This corresponds to a daily grazing impact of less than 1% on the phyto- and protozooplankton standing stock during this period. Here we also made the assumption that juvenile somatic growth is equal to the *C. finmarchicus* specific egg production rate, and that all copepods have the same P/B as *C. finmarchicus*. If we calculate the ingestion per *C. finmarchicus* female and compare it to corresponding results from weather station M in the Norwegian Sea (Irigoien *et al.*, 1998), we see that our results are slightly higher (19637 ngC f^{-1} d^{-1} in our research and 14295 ngC f^{-1} d^{-1} at station M). However, considering that the chl *a* concentration during our mid-bloom situation was twice as high as at station M and the fact that the gut fluorescence measurements at station M were not corrected for possible pigment destruction (see above), our ingestion rate based on egg production measurements during mid-bloom seems to be in the same range as the ingestion rate measured by gut pigment analysis at station M.

Application of the temperature dependent production method by Huntley and Lopez (1992), yields an average ingestion rate of 1.2 mgC m^{-3} d^{-1} during mid-bloom (Table 2 and Fig. 5B), and corresponds to an ingestion rate of 15098 ngC f^{-1} d^{-1}. This is concordant with the ingestion rate from station M (Irigoien *et al.*, 1998), and in the same range as the ingestion rate calculated from our own egg production measurements during mid-bloom. The ingestion rate corresponds to an average and negligible grazing impact of 0.6% on the phyto- and protozooplankton standing stock.

The copepod grazing pressure on the protozooplankton during mid-bloom was probably low, due to the relatively low protozooplankton biomass. The average biomass of protozooplankton during mid-bloom was approximately 3.5 mgC m^{-3}. This is much less than reported at other locations (Kattegat: Hansen, 1991; Dogger Bank: Nielsen *et al.*, 1993; Disko Bay: Nielsen and Hansen, 1995). However, at station M in the Norwegian Sea, Irigoin *et al.* (1998) found biomass values of protozooplankton in the same range as in this study, with bloom values of 4 mgC m^{-3}. The physical environment is, however, different since station M is an oceanic locality, and thus not directly comparable to the Faroe Shelf.

Of the protozooplankton only the thecate dinoflagellates increased significantly in numbers during mid-bloom with a calculated growth rate of 0.15 d^{-1}. This is similar to values reported elsewhere. Hansen (1992b) found a maximum growth rate for *Protoperidinium pellucidum* of 0.15 d^{-1}, (temperature corrected to 7°C, $Q_{10}=2.8$) and other measurements of growth rates of *Protoperidinium* spp. are in the same range (Hansen *et al.*, 1997). Using a growth rate of 0.15^{-1} for the thecate hetero-

trophic dinoflagellates, yields an average ingestion rate of 0.6 mgC m^{-3} d^{-1} during mid-bloom (Table 2 and Fig. 5) and corresponds to only 0.4% of the phytoplankton standing stock. The ingestion rate of the naked heterotrophic dinoflagellates and the ciliates is unknown, but it is unlikely to be of any significant importance due to their low standing stock and apparently low growth rates, as they did not increase in numbers.

Thus during mid-bloom the grazing impact of both the copepods and the protozooplankton on the phytoplankton seem to have been of minor importance. Hence the bulk part of the phytoplankton biomass was most likely settling out of the euphotic zone.

Conclusion

On the Faroe Shelf the importance of protozooplankton as grazers on the phytoplankton during the pre-bloom period seems to be negligible. The copepods on the other hand seem to have a large grazing potential. However, to what degree the copepods are able to suppress or postpone the phytoplankton spring bloom is unknown. During mid-bloom the estimated grazing impact on the phytoplankton by the protozooplankton and the copepods was negligible.

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