Spatial patterns of surface blooms and recruitment dynamics of *Calanus finmarchicus* in the NE Norwegian Sea

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Spatial dynamics of phytoplankton blooms and Calanus finmarchicus were analysed in a large-scale oceanic area (10 274 km) in the NE Norwegian Sea (69–71°N, 12–16°E). Data on hydrography, chlorophyll a (Chl a) and mesozooplankton (net samples and Optical Plankton Counter) were collected in surface waters (0–30 m) during spring and early summer 2003. Spatial patterns of copepodites in relation to hydrography and Chl a concentration were analysed by constrained correspondence analysis. Distribution of phytoplankton and C. finmarchicus was highly patchy. The overwintering generation (CV and adult females) had highest abundances in areas with phytoplankton blooms, whereas the recruiting cohort (CII + CIII copepodites) was found in water parcels with low Chl a concentration. Differences in recruitment dynamics between the southern and northern Norwegian Sea are discussed. Our data confirm the importance of phytoplankton spring blooms in initiating the recruitment of C. finmarchicus. This opens up for a future mapping of sea surface chlorophyll to depict the large-scale variability in the demography of C. finmarchicus during the reproductive season in the Norwegian Sea.

INTRODUCTION

According to the classical match–mismatch hypothesis, the energy transfer between phyto- and zooplankton is determined by the match or mismatch of both in time and space (Harvey, 1936; Cushing, 1974, 1975). For decades, this phenomenon has attracted attention in all types of marine pelagic communities (Colebrook, 1979; Brander and Hurley, 1992; Heath, 1995; Beaugrand *et al.*, 2003) because it is considered to be important for the efficiency of energy transfer in marine food webs.

In the North Atlantic, a substantial body of information relating to the match–mismatch hypothesis is available. The majority of this information deals with the pelagic copepod *Calanus finmarchicus* as the dominating grazer in these waters (Planque and Batten, 2000). Studies of the demography of *C. finmarchicus* and the timing of recruitment demonstrate a highly variable picture. In North Norwegian fjords, there is indeed a temporal mismatch between the peak of primary production and the most intense growth phase of herbivorous zooplankton (Hopkins *et al.*, 1984). On the shelves of the NE Atlantic, both match and mismatch scenarios are observed (Heath *et al.*, 2000). In oceanic temperate and high-latitude waters, there appears to be a better match between primary production and recruiting herbivores (Skjoldal *et al.*, 1987; Hirche *et al.*, 2001), because of a delay in the onset of the phytoplankton bloom in open waters (Colebrook, 1979). At ocean weathership M in the southern Norwegian Sea (66°N, 2°E), a near-simultaneous peak of chlorophyll and copepodites CI–CIII of *C. finmarchicus* was observed in spring 1997 during the Trans Atlantic Study of *Calanus* (TASC) (Hirche *et al.*, 2001). Very similar patterns in the timing of phytoplankton production and copepodite recruitment were also observed at weathership M 50 years ago (Halldal, 1953; Østvedt, 1955). This simultaneous peak of chlorophyll

and the recruiting cohort of *C. finmarchicus* have been attributed to cannibalism by females on their offspring (Ohman and Hirche, 2001) as well as to advective processes around the weathership (Speirs *et al.*, 2004) and might also be explained by early spawning by females during the prolonged pre-bloom in oceanic waters (Niehoff *et al.*, 1999). Because of the low spatial resolution of these studies, we cannot pinpoint the mechanisms responsible for the synchronous peak at present.

Our understanding of the factors which are responsible for the large variability in the timing of recruitment in relation to the spring bloom is in general still very limited. The often strongly heterogeneous distribution of phytoplankton might, through food-dependent reproduction rates of *C. finmarchicus*, result in an equally strong heterogeneity in the demography of *C. finmarchicus*. Most of the studies cited above have sampled at adequate resolution in time but lack spatial resolution. Today, semi-automatic sampling platforms can provide us with synoptic data on hydrography and population structure, with a very much higher spatial resolution than in earlier studies. With these platforms, we can take advantage of the fact that, during the spring bloom in northern latitudes, maximum chlorophyll concentration normally corresponds to maximum phytoplankton production and that both occur near the surface, together with maximum abundance of *C. finmarchicus* (Longhurst and Harrison, 1989).

To analyse spatial patterns of surface blooms and recruitment dynamics of *C. finmarchicus*, we selected a large-scale oceanic area (10 274 km) in the NE Norwegian Sea, within the core habitat of *C. finmarchicus* (Planque and Fromentin, 1996). We sampled this area using an undulating platform that carried hydrographic instruments, a fluorescence sensor and an Optical Plankton Counter (OPC) for *in situ* zooplankton particle enumeration. The selected study area is, in terms of logistics and costs, within reach by mid-size research vessels from port in North Norway and was covered three times, twice in May and once in June 2003.

METHODS

Two cruises we carried out in an oceanic area (>2000 m deep) northwest of Vesterålen in the northern Norwegian Sea (Fig. 1). During the cruises in spring and summer 2003 (5–15 May and 6–8 June), with R/V 'Johan Ruud' and R/V 'Jan Mayen', respectively, data on the distribution of temperature, salinity, fluorescence and zooplankton were collected. A towed vehicle (Scanfish, GMI, Denmark) with mounted OPC (Focal Technologies Inc., Canada), CTD (SBE 911, Seabird Electronics Inc., USA) and fluorescence sensor (Seapoint
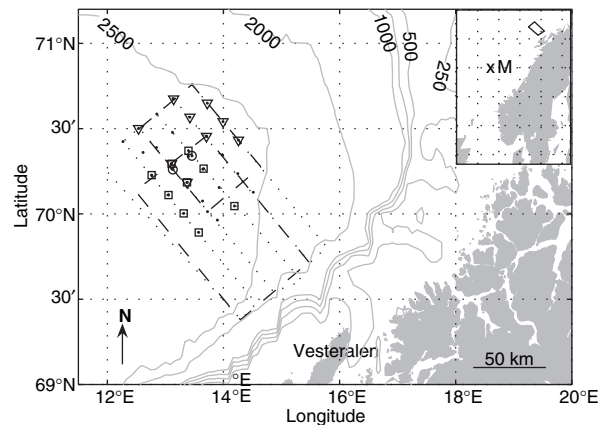
Fig. 1. The oceanic study area off Vesterålen, northern Norway. Dotted lines represent transects sampled during 10–13 May, roughly the same transects were sampled during 5–7 May (larger box) and 6–7 June (smaller box). Stations sampled for zooplankton are marked by squares (7–8 May), triangles (9–10 May) and circles (8 June). Stations sampled for chlorophyll *a* only are marked by dots. Weathership M is depicted in the overview map.

Chlorophyll Fluorometer, Seapoint Sensors Inc., USA) was operated in undulating mode along transects (Fig. 1) in the upper 60 m during May and in the upper 100 m during June. This work focuses on surface dynamics, and chlorophyll maxima were always found in the upper 30 m except in one ~20 km wide patch on only one of the transects; thus, only data from the upper 30 m are presented here. The Scanfish was towed continuously for 1–3.5 days, 5–7 May, 10–13 May and 6–7 June, respectively. During 6–7 June, only the northwestern part of the study area was covered. To calibrate the fluorescence sensor and the OPC, at 41 stations (36 stations during 7–10 May and 5 stations during 8 June), we made chlorophyll measurements and, at 21 stations (19 during 7–10 May and 2 on 8 June), vertical net hauls (WP2, 180-μm mesh size and 0.196-m mouth opening) were carried out.

Hydrography

The horizontal images of temperature and salinity were prepared by first interpolating the raw data of each 10-m layer (0–10, 11–20 and 21–30 m) using the kriging method built into Surfer (version 6.01, Waterloo Hydrogeologic, Inc.). The resulting gridded data of the three layers were then averaged and plotted using Matlab (version 6.5, The Mathworks, Inc.).

Chlorophyll

The *in vivo* fluorescence sensor on the Scanfish was calibrated with chlorophyll *a* (Chl *a*) values obtained from water samples. At each station, one water sample from 5-m depth was taken with a 5-L Niskin bottle. From this,

three replicates of 20 mL were filtered through GF/C filters. The filters were wrapped in aluminium and frozen immediately. The remaining water from the Niskin bottle was used for measurements by the fluorescence sensor on the Scanfish. Ashore, Chl *a* was analysed using a Turner Designs fluorometer and methanol as extractant (Holm-Hansen and Riemann, 1978). Corresponding Chl *a* values obtained with the Turner Designs fluorometer were then plotted against fluorescence from the Scanfish sensor and a regression line was fitted to the data by the least squares method. All fluorescence data (x) were converted into Chl *a* values (y) using the resulting regression equations ($y = 0.3965x + 0.6984$, $r = 0.72$ for the first cruise and $y = 1.7005x + 0.5291$, $r = 0.73$ for the second cruise).

Horizontal images of the distribution of Chl *a* were prepared the same way as described for temperature and salinity, but, instead of the average of the gridded data, the integrated data for the upper 30 m were plotted.

Zooplankton

Net hauls were confined to the upper 30 m because this work focused on studying the surface distribution of copepodites. During the second cruise, however, net samples were taken from the upper 100 m. On board, samples were immediately preserved in a solution of 80% seawater and 20% fixation agent (50% formalin buffered with hexamine and 50% anti-bactericide propandiol). Copepods were counted and assigned to development stages under a stereomicroscope. Abundance was calculated based on filtered volume (vertical hauling distance multiplied with mouth area), assuming 100 % filtration efficiency.

OPC data were processed using Matlab and the Matlab-based toolbox 'clione'. Size classifications of copepodite stages for each Scanfish tow were computed using the programme MIX in the form of the mixdist package for R (R Development Core Team, 2005). All OPC data collected (from 0 to 60 and 0 to 100 m, respectively) were used for this process. MIX iteratively fits distributions to data based on proportion, mean and standard deviation. The OPC used in this study had been calibrated with live zooplankton from northern Norwegian fjords in 2001 and 2002 by Edvardsen and Fossheim (unpublished data) for all development stages of *C. finmarchicus*. Their values of mean and standard deviation for the size of each copepodite stage were used as starting values for the iterative fitting process in MIX. Frequency values from net samples were assigned to starting values for proportion. Because of the limited resolution of the OPC, CI copepodites were not clearly separated from smaller zooplankton such as *Pseudocalanus* spp. and were thus excluded from our analyses. Sizes of CII and CIII copepodites clearly overlap, and they were grouped into one class, as well as CV and adult females. CIV copepodites have a relatively distinct size signature and could be resolved as one class. The resulting size classifications are summarized in Table I. Images of the horizontal distribution of copepodites were prepared in the same way as the images of the horizontal distribution of Chl *a*, i.e. data from each 10-m layer were interpolated and then integrated over the upper 30 m.

Statistical analysis

To examine the relationship between abundance of copepodite stages and environmental variables, we performed a constrained correspondence analysis (CCA, ter Braak, 1986) for each of the three time periods separately. In the CCA, Chl *a* concentration, temperature and salinity were used as constraining variables to explain the inertia in the data on copepodite abundance. Monte Carlo permutations were computed to test the significance of the constraining variables. All statistical analyses were performed using the package 'vegan' (Oksanen *et al.*, 2005) in R (R Development Core Team, 2005).

RESULTS

Hydrography

The study area was clearly dominated by Atlantic water (AW, $S > 35$, Swift, 1986) (Fig. 2). Less saline coastal water (CW, $S < 34.8$, Johannessen, 1986) occurred in two

Table I: Size classification of optical plankton counter data used in this study

Copepodite stage	Equivalent spherical diameter (mm)		
	7–10 May	10–13 May	6–7 June
CII + CIII	0.63–1.12	0.65–1.02	0.65–0.98
CIV	1.12–1.57	1.02–1.55	0.98–1.61
CV + CVI	1.57–2.0	1.55–2.0	1.61–2.0

For explanation on how the size ranges were determined, see *Methods*.
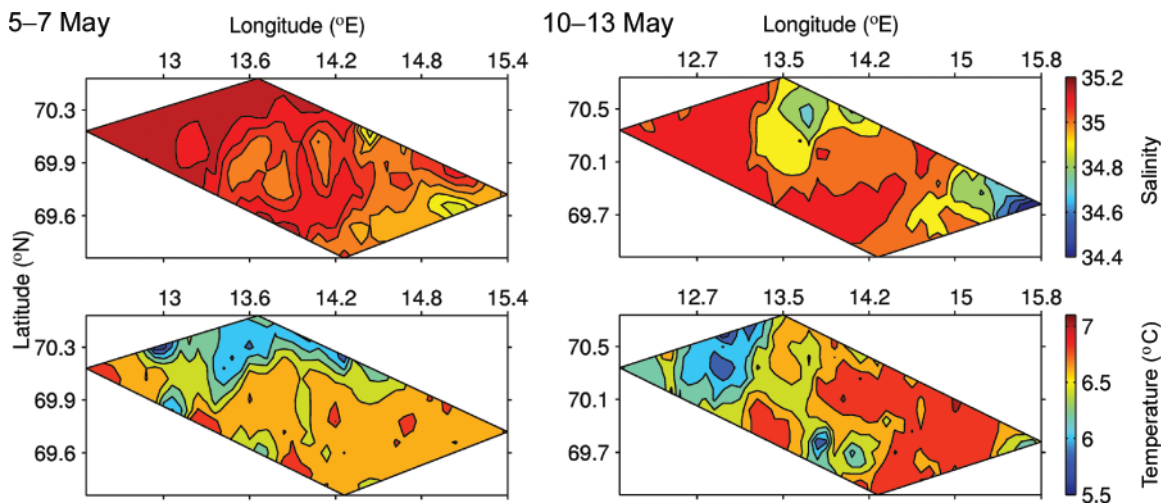
Fig. 2. Horizontal distribution of salinity (upper panels) and temperature (lower panels) in the upper 30 m of the oceanic Norwegian Sea during spring 2003. Data were collected by a CTD mounted on an undulating platform that was towed along the transects shown in Fig. 1.

small lenses in the northeastern part of the study area (Fig. 2) and extended down to a maximum of 10 m (data not shown). Mixed Atlantic and Coastal water (MW, S = 34.8–35.0; Johannessen, 1986) was found where AW and CW met (Fig. 2), down to a maximum of 45 m (data not shown). The area sampled during 10–13 May extended further northeast than that during 5–7 May. CW and MW occupied a large part of the area only sampled during 10–13 May and had then also replaced some of the AW in the eastern part of the study area. Water temperature was relatively uniform throughout the study area and ranged from 5.5 to 7.2°C (Fig. 2).

Distribution of chlorophyll

Chl a distribution was highly heterogeneous. During 5–7 May, Chl a concentration in the upper 30 m was moderate to relatively high (>7.5 mg m^{-2}) in CW and MW (Fig. 3, top left panel). Low Chl a concentrations (<5 mg m^{-2}) dominated in AW, but in patches high values were also reached (Fig. 3, top left panel). Irrespective of water mass, Chl a concentration during 10–13 May compared with that during 5–7 May had increased in the centre and in the west of the study area, whereas it had decreased in the east of the study area (Fig. 3, top panels). During 10–13 May, Chl a concentration was not linked to water mass characteristics (Figs 2 and 3). Chl a concentration during 8 June was uniformly low (<3 mg m^{-2}). These data are not shown here.

### Zooplankton community and demography of *C. finmarchicus*

The mesozooplankton community was clearly dominated by *Calanus* nauplii; during May, they constituted

~50 % of the community (Table II). *Calanus finmarchicus* was the dominant zooplankton species both in spring (~20%) and summer (~40%). *Oithona* spp., *Pseudocalanus* spp. and *Oikopleura* spp. were also of quantitative importance in spring and summer. Young stages of *Calanus hyperboreus* made up ~3% in spring. In summer, Hydrozoa increased in importance and amounted to >20% of the zooplankton community.

In May, the *C. finmarchicus* population in the upper 30 m was dominated by nauplii and CI copepodites (Fig. 4). During 9–10 May, the relative importance of CIV copepodites had increased slightly compared with 7–8 May (Fig. 4). In June, CIV copepodites were clearly the dominant stage in the upper 100 m (Fig. 4).

Distribution of copepodites

Both in May and June, the distribution of all developmental stages in the upper 30 m was more closely linked to Chl a concentration than to water mass characteristics (Figs 2, 3 and 5). In May, stages of *C. finmarchicus* were clearly separated in the ordination plots (Fig. 5). High abundances of young copepodite stages were observed in areas with low Chl a concentration (Fig. 3), CIV copepodites were associated with intermediate Chl a concentrations and stages CV and CVI had the highest abundances in areas with phytoplankton blooms (Chl a concentration > 7.5 mg m^{-2}). During 5–7 May when high Chl a concentration was associated with low salinity waters (Figs 2 and 3), both Chl a concentration and salinity were associated with the first ordination axis that explained over 60% of the inertia in the data (Fig. 5). During 10–13 May when Chl a concentration was not linked to water mass characteristics,
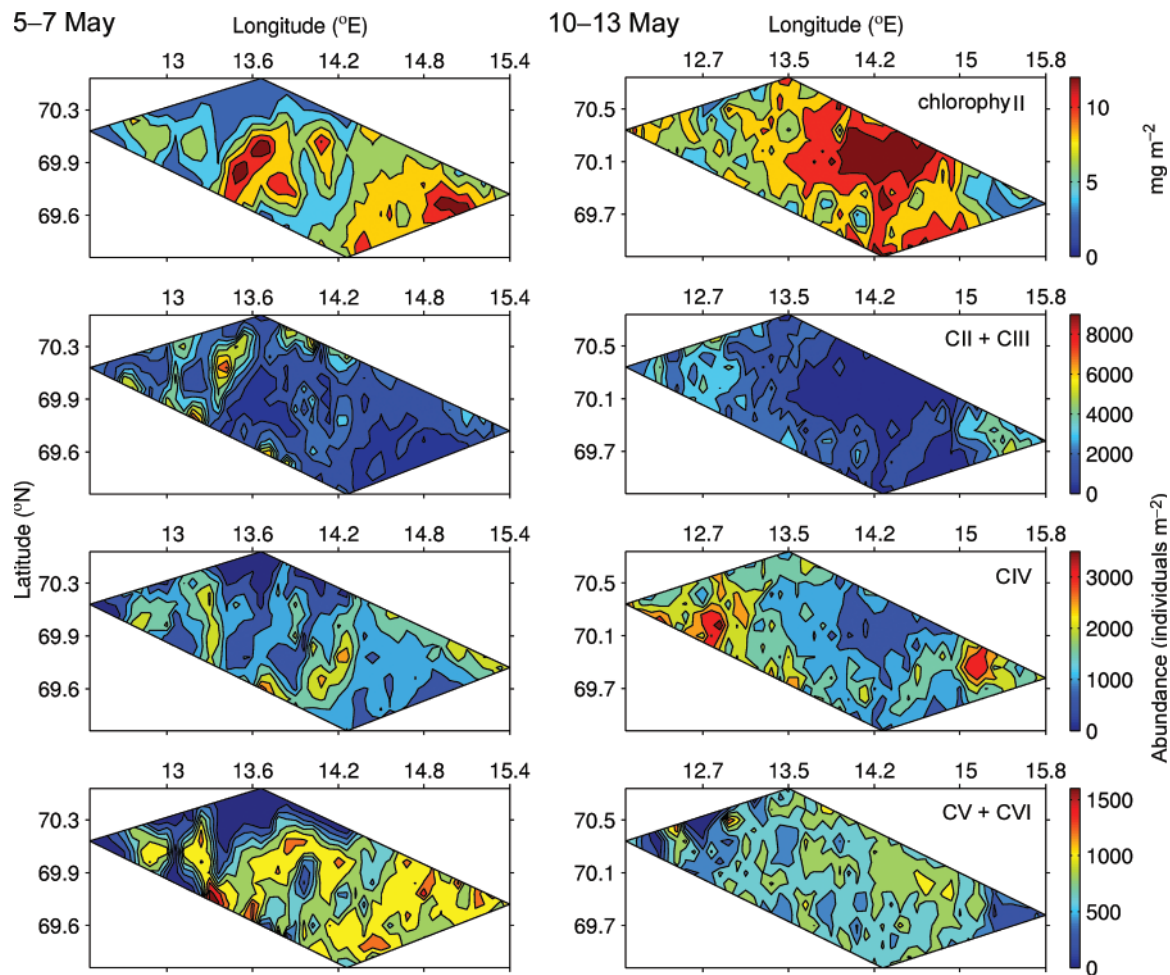
Fig. 3. Horizontal distribution of chlorophyll *a* and *Calanus finmarchicus* copepodites during spring 2003 in the oceanic Norwegian Sea integrated over the upper 30 m. Data were collected along the transects depicted in Fig. 1 by an undulating platform equipped with a fluorescence sensor and an Optical Plankton Counter.

patches with equally high abundance of young copepodites were found in CW, MW and AW. During this period, only Chl *a* concentration was associated with the first ordination axis, whereas salinity was associated nearly only with the second ordination axis that explained only 0.8% of the total inertia in the abundance data (Fig. 5). The effect of temperature on the distribution of *C. finmarchicus* stages in May was secondary to the effect of Chl *a* concentration as can be seen from the projection of the temperature and Chl *a* concentration arrows on the first ordination axes (Fig. 5). Because of the uniformly low Chl *a* concentration in June, a very uniform distribution pattern of copepodites was observed (data not shown). Total inertia in the June data was low compared with that May (Table III). The constraining factors salinity, temperature and Chl *a* concentration

explained little of the total inertia in the June data but were nevertheless significant (Table III, Fig. 5).

Grazing pressure

In areas where CI–CIII copepodites were dominant, i.e. found in abundances more than three times the abundance of CIV–CVI copepodites, the grazing pressure estimated by the Chl *a* : phaeophytin ratio was significantly lower than in areas where older copepodites were dominant (*t*-test, $P = 0.018$, $n = 19$).

DISCUSSION

This study focused on *C. finmarchicus*, which also from net samples proved to be the dominant zooplankton in the

Table II: Composition (in %) of the mesozooplankton community off Vesterålen in spring and early summer 2003

| Species	5–7 May	13–14 May	8 June
Calanus spp. nauplii	54.15	49.98	0.02
Calanus finmarchicus	18.91	23.17	41.27
Calanus hyperboreus	2.72	3.49	0.11
Pseudocalanus spp.	3.95	4.07	7.82
Microcalanus spp.	0.14	0.02	0.39
Oithona spp.	13.07	12.74	12.87
Oncaea spp.	1.66	1.54	4.45
Temora spp.	0.11	0.02	0
Acartia spp.	0.75	0	0.02
Metridia spp.	0.02	0.01	0.01
Parathemisto spp.	0.06	0.06	0.11
Euphausiacea	0.15	0.25	0.67
Ostracoda	0.01	0.03	0.24
Hydrozoa	0.35	0.31	23.18
Chaetognatha	0.75	1.11	2.37
Oikopleura spp.	3.21	3.10	6.37
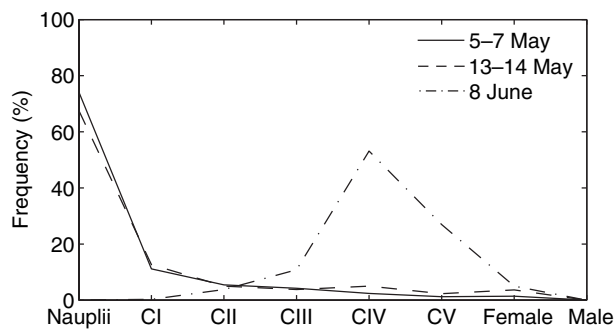
Fig. 4. Population dynamics of *Calanus finmarchicus* in spring 2003 in the oceanic northern Norwegian Sea.

study area. Low species diversity of zooplankton in the Nordic Seas makes it possible to distinguish species and even development stages by applying size limits to data collected by the OPC. Size classifications applied here were computed according to a MIX analysis (Macdonald and Green, 1988) based on data from an earlier calibration of the OPC used in this study (Edvardsen and Fossheim, unpublished data). Adult *Pseudocalanus* spp. were the only additional species of quantitative importance in our study area that overlaps in size only with copepodite stage CI of *C. finmarchicus* (Edvardsen *et al.*, 2002). Therefore, CI copepodites were excluded from our OPC analyses, and we consider the defined size classes as reliable representations of CII–CVI stages of *C. finmarchicus*.

Our data confirm that we indeed encountered the recruitment period of *C. finmarchicus* during the field surveys. In early-to-mid May, the majority of the population comprised naupliar and early copepodite stages, whereas in early June the majority of the sampled population had reached copepodite stage IV. Although older copepodites may have inhabited deeper water layers in May, when net samples were taken from 0 to 30 m only, the progression through stages agrees with an expected population development during the recruiting period (Tande, 1982). The observed timing, however, is earlier than expected for the NE Norwegian Sea (Pedersen *et al.*, 2000; Dale *et al.*, 2001; Arashkevich *et al.*; 2004) and more closely resembles the timing on the shelves (Arashkevich *et al.*, 2004) and in the southern Norwegian Sea (Heath *et al.*, 2000; Hirche *et al.*, 2001). The large-scale data from 5 to 7 May demonstrate that the recruiting generation (G_1) was established as early in oceanic as in coastal waters. In fact, during 5–7 May, highest abundances of CII and CIII copepodites were found in oceanic water in the northwestern part of the study area. Grazing pressure of the overwintering generation was high, indicating a high resource demand of reproducing females. In early-to-mid May, the G_0 generation (CV copepodites and adult females) was found in water parcels with high Chl *a* concentration. Five-fold higher numbers of the G_1 generation were found in water with low Chl *a* concentration, demonstrating a pronounced patchy distribution of the recruiting generation in the NE Norwegian Sea.

A

B

C
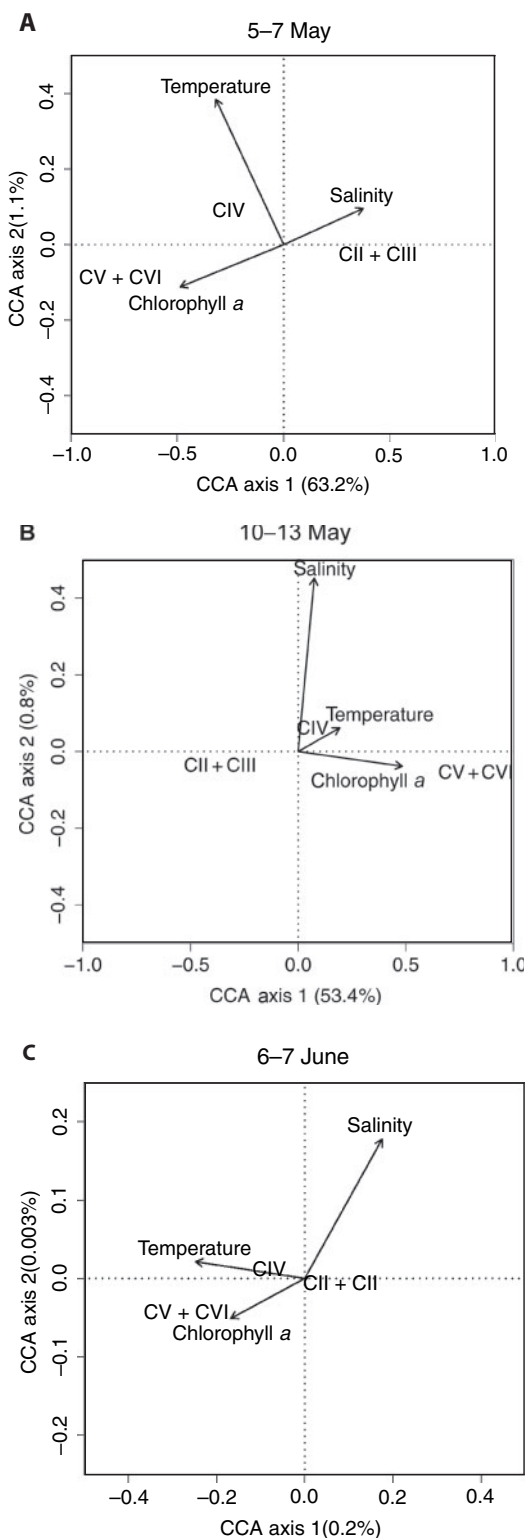
Fig. 5. Ordination plots of constrained correspondence analyses of *Calanus finmarchicus* copepodite abundance (cop) as a function of temperature (*T*), salinity (*S*) and chlorophyll *a* concentration (Chl *a*): cop ∼ *T* + *S* + Chl *a*.

The ratio between what we interpret as the G_1 and G_0 generations agrees with an expected ratio between females and CI–CIII copepodites during the recruitment period (e.g. Skjoldal *et al.*, 1987; Hirche *et al.*, 2001). Cannibalism of females on eggs and naupliar stages (Basedow and Tande, in press) may also fine-tune the demographic scheme of recruits and could thus result in lower abundances of CI–CIII copepodites in patches with high abundance of females. Cannibalism alone, however, cannot explain the overall spatial patchiness of CI–CIII copepodites and females, which was observed in the NE Norwegian Sea. If cannibalism was partly responsible for the horizontal segregation of the G_1 and G_0 generations, an underlying patchiness of females would additionally be required to create the observed patterns.

Advection clearly played a role in the study area, where a strong northward current with a typical speed of 20–30 cm s^{-1} prevails (Blindheim, 2004). Considerable bodies of surface water were replaced by water with slightly higher temperature and lower salinity between 5–7 and 10–13 May. This exchange of water masses, however, appeared not to affect understanding of the overall dynamics of phytoplankton and recruitment. Even though during 5–7 May phytoplankton blooms were associated with CW and MW, correspondence analyses clearly showed that both temperature and salinity were of secondary importance in explaining the inertia in the abundance data of 5–7 and 10–13 May. Instead, recruitment dynamics of *C. finmarchicus* were strongly linked to spatial dynamics of phytoplankton blooms. The field data presented here are one of the very few data sets available with high spatial resolution during the spring bloom period in the Norwegian Sea. The observed high degree of small- and mesoscale patchiness in the distribution of Chl *a* and *C. finmarchicus* recruits supports the view of Speirs *et al.* (Speirs *et al.*, 2004), who modelled population dynamics of *C. finmarchicus* at weathership M and concluded that correct vital rates from *in situ* population studies are unlikely to obtain without taking phytoplankton patchiness and advection into account.

The mismatch between the phytoplankton bloom and high surface abundance of young *C. finmarchicus* copepodites, which was observed in our data, resembles the mismatch observed in northern coastal areas (Fig. 6, top) and contrasts with the match observed at weathership M (Fig. 6, bottom) and at several shelf break sites bordering the Norwegian Sea (Heath *et al.*, 2000). The question arises what causes this match in some areas and the mismatch in other areas.

Seawater temperature in Balsfjorden in the 1970s was between 2 and 4°C (Tande, 1979), whereas generally

Table III: Results of the constrained correspondence analyses

Inertia	5–7 May	10–13 May	6–7 June
Total	0.3606	0.3339	0.0522
Constrained	0.2321	0.1808	0.0097
Unconstrained	0.1286	0.1531	0.0425
P-value	<0.001	<0.001	<0.001

Copepodite abundance (cop) was modelled with temperature (T), salinity (S) and chlorophyll a concentration (Chl a) as constraining factors: cop $\sim T + S +$ Chl a.
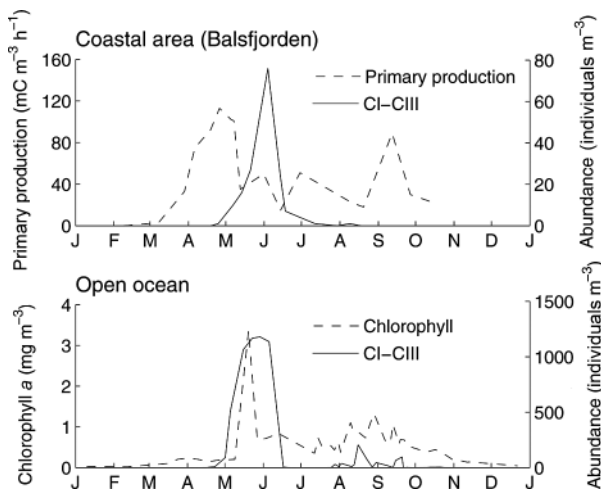

Fig. 6. Succession of phytoplankton bloom and recruitment of *Calanus finmarchicus* CI–CIII copepodites in a coastal area in northern Norway (top) and at oceanic weathership M in the southern Norwegian Sea (bottom). Data from H.-C. Eilertsen (top, phytoplankton), K. Tande (top, zooplankton) and redrawn from Hirche et al. (Hirche et al., 2001) (bottom).

higher temperatures prevail on the shelves of the Norwegian Sea. Higher temperatures will tend to narrow the delay between peak spawning and peak of young copepodites because of higher developmental rates. Together with high egg production rates during the pre-bloom (Niehoff et al., 1999), higher temperature may thus promote a match between spring bloom and the recruiting cohort.

We interpret the match observed at weathership M to be generated by a combined effect of cannibalism and relaxed grazing pressure because of declining abundances of G_0 females. Both cannibalism and high grazing pressure are significant during the spring bloom as long as high abundances of females prevail. The disappearance of females facilitates the often observed increase in surface chlorophyll simultaneously with a development of recruiting CI–CIII copepodites.

In our oceanic study area, however, a mismatch between the phytoplankton bloom and high surface abundances of CI–CIII copepodites was observed. In

the North Atlantic, there is a lag in the onset of the phytoplankton bloom with increasing latitude, which is related to delayed water column stratification (Sverdrup, 1953; Siegel et al., 2002). This lag is distinct from 35 to 50°N, but it is only marginal further north, i.e. in the order of a few days between 66 and 70°N (Braarud et al., 1958; Siegel et al., 2002). This surprisingly synchronous start of the phytoplankton bloom between 66 and 70°N is supposedly related to longer days at higher latitudes (Eilertsen, 1993). If in the Norwegian Sea 12-h light triggered the ascent of *C. finmarchicus* to the surface, as suggested by Speirs et al. (Speirs et al., 2005) modelling the distribution of the population in the North Atlantic, then copepods would ascend around the vernal equinox in waters from 66 to 70°N. The number of over-wintering *C. finmarchicus* is high both at weathership M and off Vesterålen and at both locations the over-wintering population consists of ~20% CIV copepodites and 75–85% CV copepodites (Halvorsen et al., 2003; Heath et al., 2004; Edvardsen et al., 2006). Therefore, in oceanic surface waters, there might be a very similar situation in the southern Norwegian Sea at weathership M and in the northern Norwegian Sea off Vesterålen when it comes to the timing of the start of the phytoplankton bloom, the timing of ascent to surface waters and the demography of the ascended population. However, similar timing of the ascent to the surface and similar stage composition may not translate directly into a synchronization of maturation and reproduction of females in the southern and northern Norwegian Sea. During spring spawning in 1997, females with mature gonads peaked in April in the southern Norwegian Sea (Pasternak et al., 2004); thus, large numbers of females spawned during the pre-bloom (Niehoff et al., 1999). In the northern Norwegian Sea, two less-pronounced peaks of mature females were observed in April and May (Pasternak et al., 2004), indicating that the population further north may be well adapted to the variability of phytoplankton spring blooms in these waters. The apparent patchiness in the onset of the phytoplankton bloom in the NE Norwegian Sea may be attributed to heterogeneity in the occurrence and germination of overwintering diatom spores

(Eilertsen and Wyatt, 2000). Our data confirm the importance of phytoplankton spring blooms in initiating the recruitment of *C. finmarchicus*. This opens up the possibility for future mapping of sea surface chlorophyll to depict the large-scale variability in the demography of *C. finmarchicus* during the reproductive season in the Norwegian Sea.

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