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Feeding, reproduction and seasonal development of *Calanus finmarchicus* in relation to water masses and phytoplankton in the southern Norwegian Sea

Eilif Gaard and Karina Nattestad

ABSTRACT

In the southern Norwegian Sea, two different water masses dominate in the upper layers: cold water from the East Icelandic Current in the western part and warmer Atlantic water in the eastern and southernmost part. In spring the stratification is stronger in the cold East Icelandic Current Water (EICW) than in the Atlantic Water (AW) and the phytoplankton biomass usually increases earlier in spring in the EICW than in the AW. In both water masses the copepod *Calanus finmarchicus* is the dominant secondary producer. The paper describes horizontal, interannual, and seasonal variability in *C. finmarchicus* in relation to hydrography and phytoplankton in the AW and EICW. Abundance, maturity, reproduction and ingestion rates of *C. finmarchicus* in spring and seasonal development of the copepod in these two water masses are described and related to phytoplankton and hydrography. The reproduction of *C. finmarchicus* starts significantly earlier in spring in the AW than in the EICW, and 2 generations are produced in the AW while only on is produced in the EICW. Measurements in May 2002 have showed that in despite of high phytoplankton concentrations in the EICW, the phytoplankton mean ingestion rate was in average 1.7 times higher in the AW. Also the mean proportion of mature females was 1.7 times higher and the mean egg production rate was 1.8 times higher in the warm AW than in the cold EICW.

Key words: *Calanus finmarchicus*, stage development, maturity, egg production, gut fluorescence, phytoplankton, Norwegian Sea

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INTRODUCTION

The upper water layer (about 500 m) in the southern Norwegian Sea consists of two different water masses. In the eastern part is warm and saline Atlantic Water (AW), entering the Norwegian Sea from southwest. About 50% of this water is flowing through the Faroe-Shetland Channel into the Norwegian Sea and the other about 50% is transported by the eastwards going Faroe Current to the north of the Faroes and into the Norwegian Sea (Hansen and Østerhus, 2000). In the western part of the Norwegian Sea the East Icelandic Current transports cold and low saline East Icelandic Current Water (EICW) southwards and then eastwards to the north of the Faroes (Figure 1). Thus, cold EICW covers the western part of the southern Norwegian Sea while Warm AW covers the eastern part and southernmost part. To the north of the Faroes, the cold and warm water masses are separated by a sharp front, termed the Iceland-Faroe Front (Hansen and Østerhus, 2000).

Below about 500 meters depth the Norwegian Sea contains cold Norwegian Sea Deep Water.

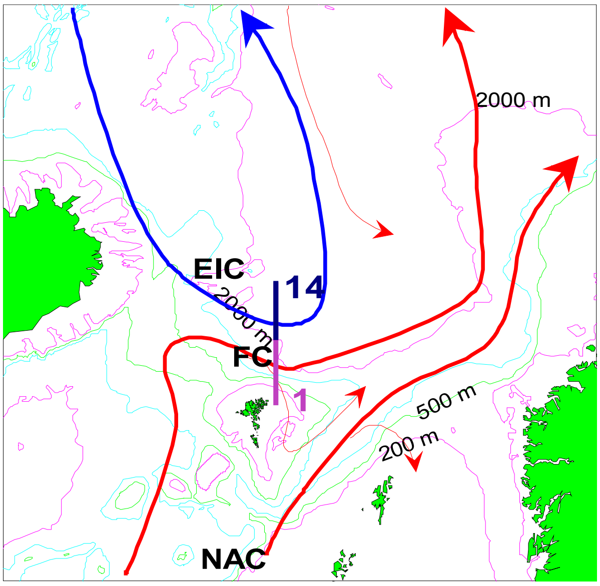


Figure 1. Topography and main current features in the upper 500 meters in the southern Norwegian Sea. The figure also shows the section from which data are presented (14 stations). EIC: East Icelandic Current, FC: Faroe Current, NAC: North Atlantic Current

Calanus finmarchicus is the dominant secondary producer in the Norwegian Sea. During spring and summer it resides in the upper layer where it feeds mainly on the phytoplankton, reproduces and grows. During this time it serves as food for several pelagic fish stocks that have their feeding migration in the area. These are *e.g.* Norwegian spring spawning herring (*e.g.* Misund *et al.*, 1998, Dalpadado *et al.*, 1998), mackerel (Reid *et al.*, 1997; Belikov *et al.*, 1998), blue whiting (Bailey, 1982; Bjelland and Monstad, 1997) and Atlantic salmon (Hansen and Jacobsen, 2000; Jacobsen and Hansen, 2000.

During winter, when the food is scarce at the surface, *C. finmarchicus* resides in diapause, as copepodite stage IV and V, in cold deep water. The main overwintering area in the North-east Atlantic is the deep Nordic Seas, at depths between 500 and 2000 m (*e.g.* Østvedt, 1955; Hirche, 1991; 1996a; Heath *et al.*, 2000a). The overwintering individuals are not feeding but survive due to low metabolic rates (Ingvardsdóttir *et al.*, 1999) relying on stored energy. Lipids, mostly deposited as wax esters in oil sacs prior to descending to overwintering depths, are the main source of energy for the overwintering period (Hirche, 1996a;b; Jónasdóttir 1999; Heath & Jónasdóttir 1999). In late winter and spring it ascends and reproduces (*e.g.* Niehoff *et al*., 1999; Gaard and Hansen, 2000; Gislason and Astthorsson, 2000; Niehoff and Hirche, 2000). The energy required to reproduction mainly comes from ingested food (*e.g*. Hirche, 1996b and references therein, Niehoff *et al*., 1999; Niehoff and Hirche, 2000); however, lipid stores are also considered to be important energy source right after ascendance to the surface in spring (Cabal *et al.*, 1997; Richardson *et al*., 1999; Rey-Rassat *et al*., 2002).

Earlier studies have indicated that the timing of spring spawning of *C. finmarchicus* is different in the AW and EICW to the north of the Faroe Islands. Spring spawning seems to occur earlier in the warm AW than in the cold EICW, resulting in different life cycles and stage composition in these two water masses (Gaard, 1996). In the warm water there are two generations: one big lasting from spring to mid summer and one smaller from mid summer to autumn, while in the cold water there is only one generation per year.

In this paper we compare environmental parameters (hydrography and phytoplankton biomass) and reproductive related parameters (stage composition, egg production, female maturity and female ingestion rates) in spring in the warm and the cold water masses in the southwestern Norwegian Sea and describe interannual variability/similarities in these two water masses.

MATERIALS AND METHODS

Hydrography, phyto- and zooplankton biomass and *Calanus finmarchicus* abundance are measured at a section along 6°05´W, from 62°20´N to 64°30´N since 1990. The section contained 14 stations and the distance between the stations was 10 NM. In May 2002 egg production, maturity and gut fluorescence of *C. finmarchicus* females were furthermore studied. In addition, hydrography and phytoplankton in a wider area in the southern Norwegian Sea in May 1996-1998 are presented.

Temperature and salinity were obtained by CTD. An EG&G CTD was used May 1995 and a Seabird Electronics 911plus CTD afterwards. The salinity was calibrated against standard seawater, analysed on an Autosal 8400A salinometer. *In situ* fluorescence was measured with Sea Tech fluorometers, interfaced to the CTD and the fluorescence was calibrated against selected samples that were analysed for chlorophyll *a*, according to the method by Baltic Marine Biologists (1979) and equation by Jeffrey and Humprey (1975).

Copepods were sampled by vertical hauls from 50 meters depth to the surface. A Hensen net was used in 1990-1991 and a WP2 net since 1992. Both nets had a mesh size of 200 µm and the towing speed was 0.3-0.5 m sec^{-1}.

Phytoplankton ingestion was estimated from gut fluorescence multiplied by the gut clearance rate (Mackas and Bohrer, 1976). Subsamples for gut fluorescence measurement were taken immediately after sampling, quick frozen with freezing spray and stored in a freezer. On the laboratory 30 females, distributed into 6 replicates of 5 females per station were extracted in 5 ml 90% acetone for and 24 hours. The gut fluorescence of *C. finmarchicus* females was measured with a Turner Designs fluorometer. The fluorescence was calibrated against standard chlorophyll *a*. The fluorescence measurement methodology and calculations of gut content and ingestion rates were according to Båmstedt *et al*. (2000) and the gut clearance rates were estimated from the temperature (Dam and Peterson, 1988).

Gonad maturity was determined from formaldehyde preserved females according to the method by Niehoff and Hirche (1996). A mean number of 55 females were determined per station. The oocytes were graded into 4 different stages, from GS1 as immature females to GS4, which characterised mature females ready to spawn.

For measuring of the egg production rates, live *C. finmarchicus* were collected with the WP2 net, equipped with a plastic bottle as a cod end. A mean number of 11 healthy females per station were transferred into 0.5 litre incubation chambers equipped with false bottom (mesh size 500 µm) to separate eggs from female and incubated at *in situ* temperature for 24 hours. The sea water in the incubation chambers was filtered through a 80 µm mesh net before it was used. After incubation, the chamber content was filtered through a 30µm mesh net and the eggs counted.

Samples used for enumeration were preserved in 4% formaldehyde. In the laboratory subsamples were taken out with a plankton splitter and were then identified and counted.

For dry weight measurements the samples were dried at 60-65°C until they reached constant weight.

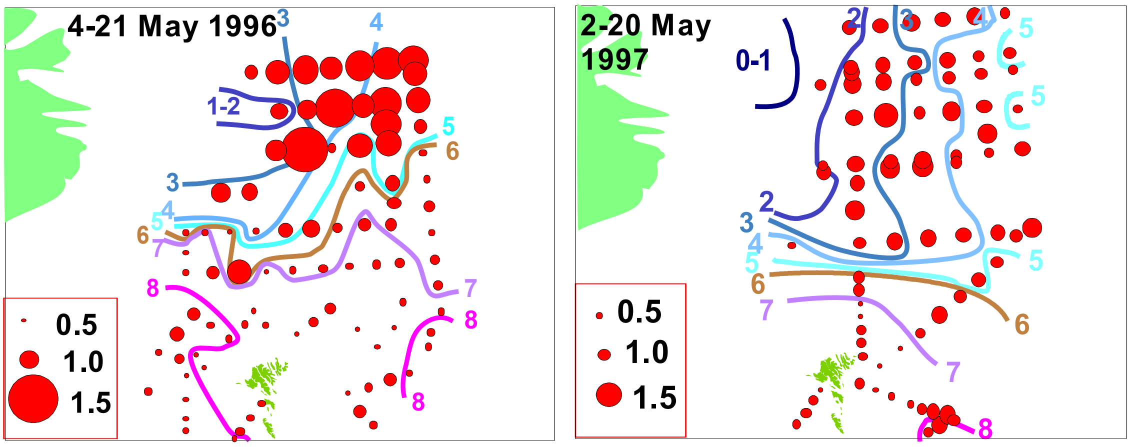
RESULTS

Hydrography and phytoplankton

The strengths of the Faroe Current and the East Icelandic Current are variable between years. In some years the EICW covers a large part of the area to the north of the Faroes, in other years it covers a smaller area. This is illustrated in three examples on Figure 2. The difference in surface temperature between the AW and the EICW in May usually is about 4-5°C.

During spring the stratification (density gradient) in the surface layer is higher in the EICW that in the AW.

Usually the spring bloom develops earlier in the EICW than in the AW, and in May the phytoplankton biomass is significantly higher in the EICW than in the AW (Figure 2).



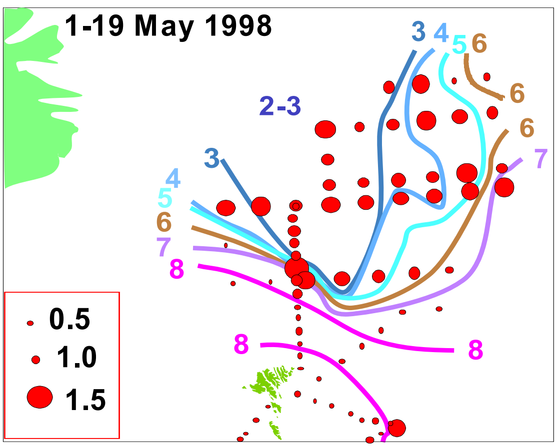


Figure 2. Temperature at 50 m depth (isolines) and mean chlorophyll *a* concentrations (µg l^{-1}) in the upper 50 m (dots) in May 1996-1998.

***Calanus finmarchicus* in relation to the environment in spring 2002**

In May 2002 detailed studies of *Calanus finmarchicus*, hydrography and phytoplankton biomass were carried out along the section shown in Figure 1. The two southernmost stations on the section covered Faroe shelf water, stations 3-7 covered oceanic Atlantic Water (AW), transported eastwards by the Faroe Current and station 9-14 covered colder East Icelandic Current Water (EICW) (Figure 3). Station 8 was located close to the front and contained a mixture of the two water masses.

Hydrography and phytoplankton

The mean temperature in the upper 50 meters of the oceanic water masses (the AW and EICW) was 7.6 and 3.8°C respectively. In the AW the stratification was low and the phytoplankton biomass was still at a low level while the EICW had a higher temperature difference in the upper layer and significantly higher phytoplankton biomass (Figure 3). The mean chlorophyll *a* concentrations in the upper 40 meters of the two water masses were 0.6 and 2.2 $\mu g\ l^{-1}$ respectively.

Abundance and stage composition

The reproduction of *C. finmarchicus* seems to have started significantly earlier in the AW than in the EICW. In the AW recruits dominated, mostly as copepodite stages CI and CII and the number of overwintered individuals (CV and CVI) was low. About 80% (by numbers) were CI-CIII (recruits). On contrary, *C. finmarchicus* in the EICW was dominated by overwintered individuals (~ 85%) and the number of recruits was low (Figure 3).

Reproduction

The female gonad maturity varied between the stations and was generally higher in the AW than in the EICW (Figure 3). In average 70% of the females in the AW and only 42% of those in the EICW were mature. The egg production rates also varied between stations, and were generally higher in the AW than in the EICW (Figure 3). In average the egg production was 9.3 eggs female^{-1} day^{-1} in the AW while it was 5.2 eggs female^{-1} day^{-1} in the EICW. However, since the number of females was higher in the EICW than in the AW the mean total egg production was roughly the same in both water masses (~650 eggs m^{-3} day^{-1}). Taking into account the proportions of mature females, the average egg production per mature female was quite similar in AW and EICW (13 and 12 eggs female^{-1} day^{-1} respectively).

Ingestion

Despite the lower phytoplankton concentrations in the AW than in the EICW the gut content generally was higher in the AW (Figure 3). Due to the higher temperature in the AW than in the EICW the gut clearance rate is also higher in that water mass, and the ingestion rate was clearly higher in the AW than in the EICW. In average the ingestion rate in the AW was about 80 ng chl. *a* equiv. female^{-1} day^{-1} while it was about 46 ng chl. *a* equiv. female^{-1} day^{-1} in the EICW.

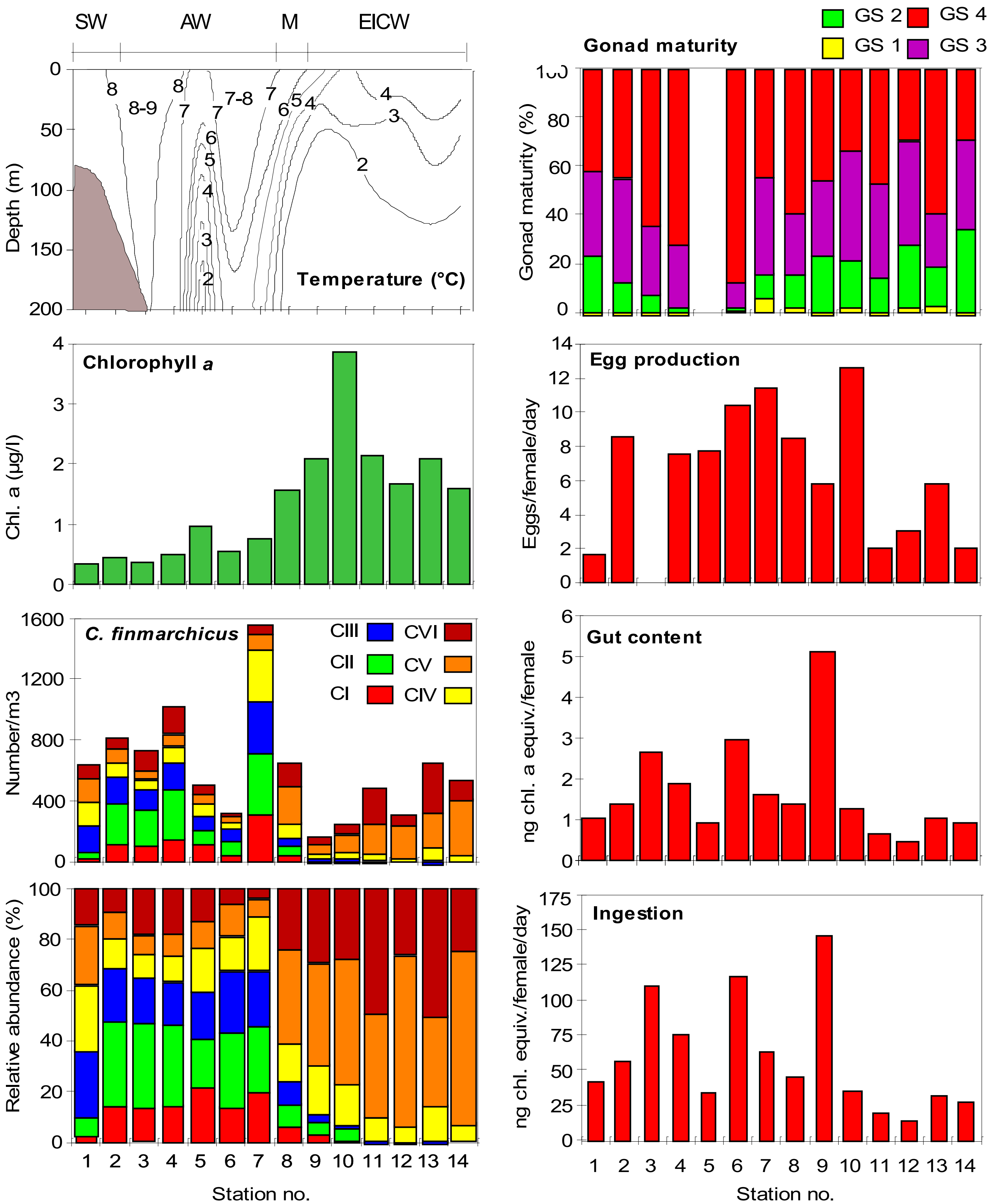


Figure 3. Left panels: Temperature, mean chlorophyll *a* concentrations at 5, 20 and 40 m depth and absolute and relative abundance of *Calanus finmarchicus* in the upper 50 m of the water column. Right panels: Proportion of female gonad maturity stages, egg production rates, gut chlorophyll content and ingestion rates by *C. finmarchicus* females in the upper 50 m of the water column along the section shown in Figure 1 on 10-11 May 2002.
SW: Shelf Water; AW: Atlantic Water; M: Mixed Water; EICW: East Icelandic Current Water.

Interannual variability during spring

Differences in phytoplankton development and *Calanus finmarchicus* stage composition and abundance between the two water masses has been observed almost every year since the monitoring started in 1990. Almost every year the phytoplankton production starts earlier in the EICW than in the AW. There is, however, observed large variability between years (Figure 4). The reason for this regional difference and interannual variability most likely is regional and interannual differences in stratification of upper mixed layer (Figure 4).

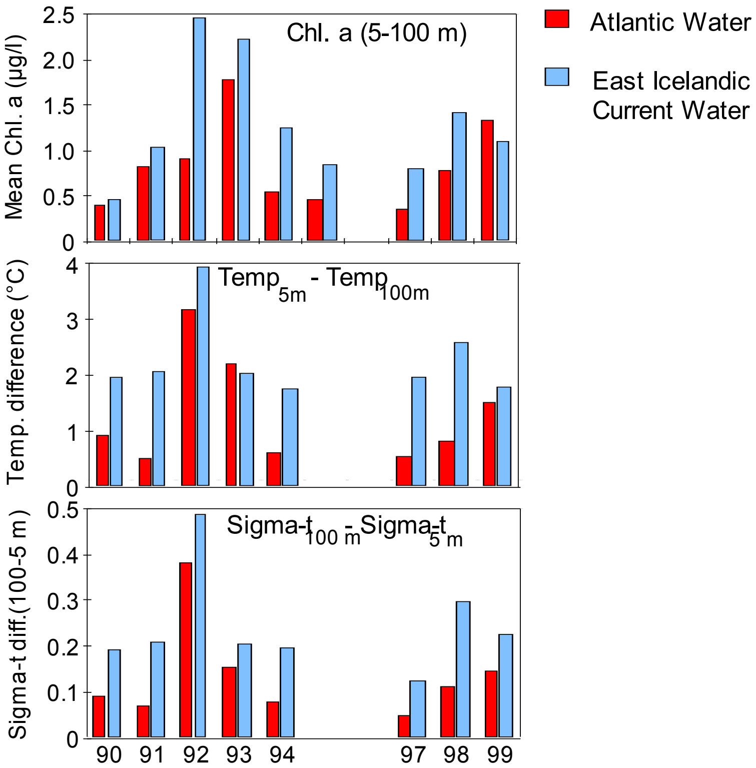


Figure 4. Mean chlorophyll *a* concentrations and temperature and density differences between 5 and 100 m depth in Atlantic Water and East Icelandic Current Water at the section shown in Figure 1 in mid-late May 1990-1999.

The abundance and the stage composition of *C. finmarchicus* in the two water masses have also been different every year since 1990, when the monitoring started (Figure 5). In the AW *C. finmarchicus* in May was always dominated by young copepodite stages (recruits), indicating that there has been reproduction in that water mass for some time prior to the samplings. The EICW was, on the other hand, dominated by overwintered individuals, mainly as CV and adults (largely females). Recruits are always scarce in the EICW in May, and very few nauplii found here, indicating that the reproduction in this part of the section had not reached the peak spawning period. The proportion between CV and adults in May was close to 1:1 in the EICW, indicating that the moulting process to adults was still going on. This is not the case in the AW where the proportion of CV compared to adults always was much lower (Figure 5).

The total zooplankton biomass also fluctuated much between years (Figure 6). The biomass was almost always clearly higher in the EICW than the AW, partly because of its dominance of larger copepodite stages (overwintered) and partly because other large-sized copepods usually also occur in the EICW. This is mainly *Calanus hyperboreus*, which may occur in 1-10% (by numbers) and to less extent another coldwater copepod species, *Metridia longa*. These copepods are even larger than *C. finmarchicus* and may affect the total zooplankton biomass much in the EICW.

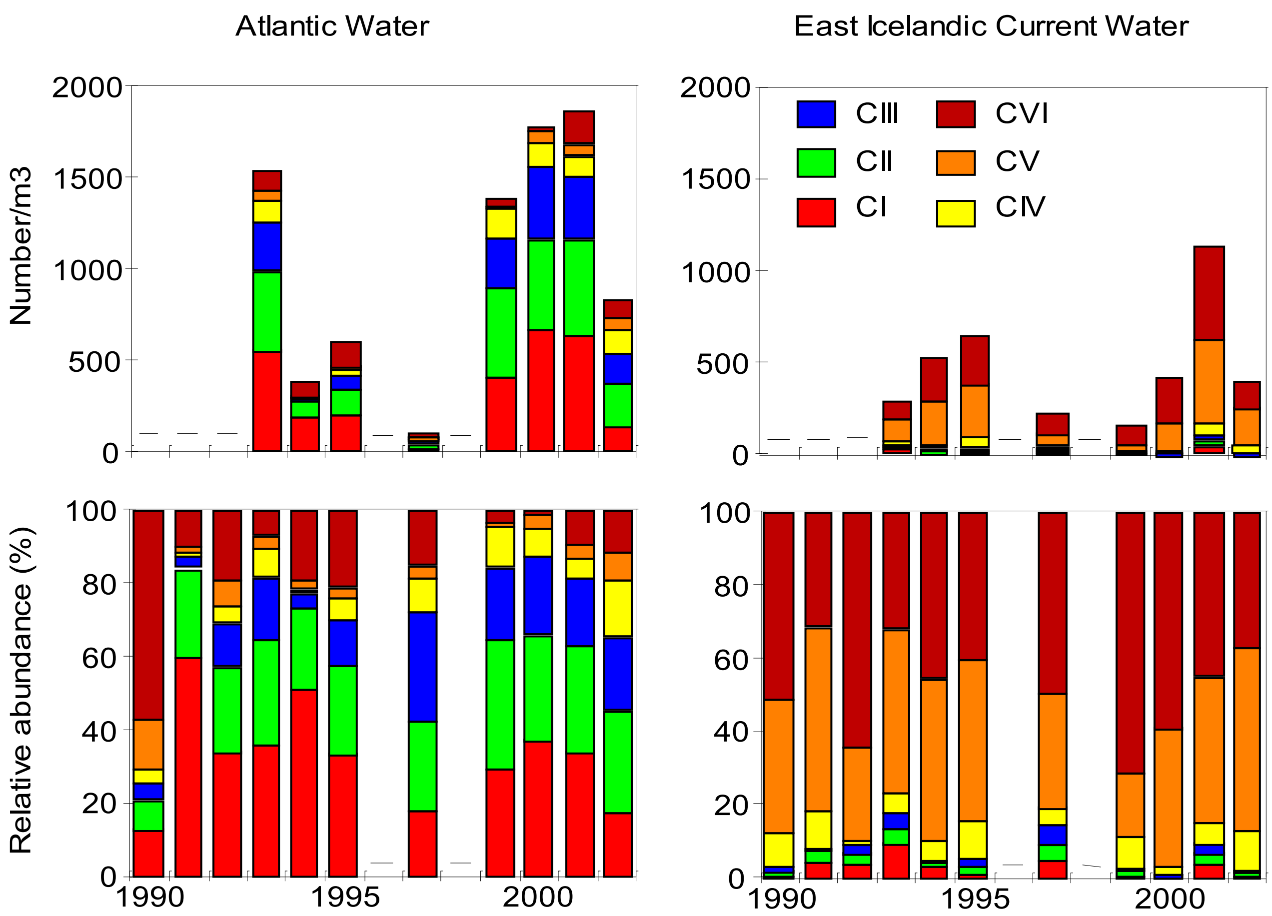


Figure 5. Absolute (upper panels) and relative (lower panels) of *Calanus finmarchicus* stages in the upper 50 of the water column in AW (left panels) and EICW (right panels) in the section shown in Figure 1 in May 1990-2002. —: no data are available.

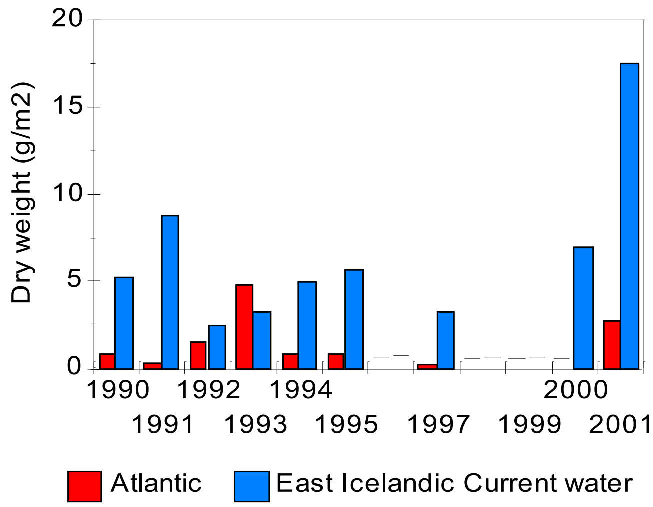


Figure 6. Zooplankton biomass the upper 50 of the water column in the AW and EICW along the section shown in Figure 1 in mid-late May 1990-2001. -: No data available.

Seasonal development of Calanus finmarchicus

Due to the different timing of spawning of *C. finmarchicus* during spring and different stage duration in the AW and EICW, the seasonal development is quite different in the two water masses. This is illustrated in the example from 1995 (Figure 7). In the AW the spring spawning started prior to the spring bloom and main reproduction most likely has been in April-May. In September a new smaller generation appeared in the upper layer, mostly as copepodite stage IV. In the EICW the spawning has started much later at only one generation occurred. Most like the peak spawning has been in mid summer.

Most of the productive season the abundance was higher in the AW but due to larger individuals, the zooplankton biomass was higher in the EICW.

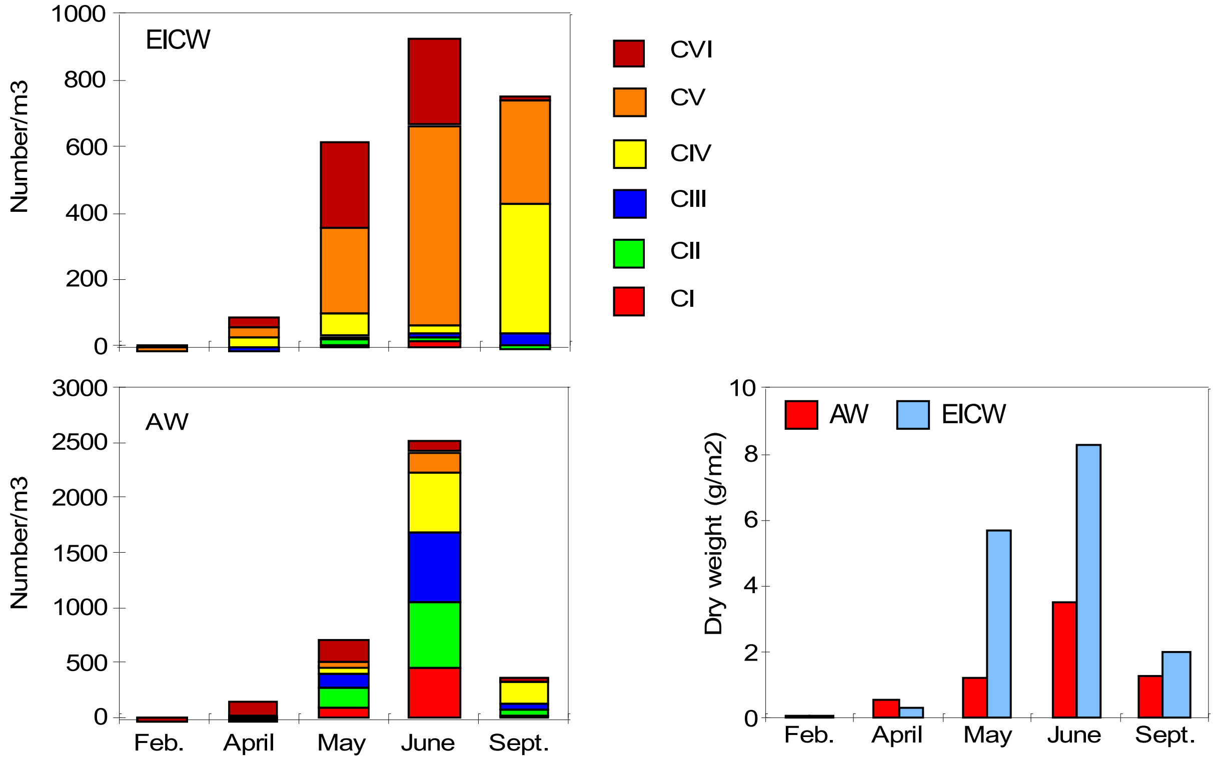


Figure 7. Abundance of *Calanus finmarchicus* copepodite stages in EICW and AW (left panels) and zooplankton biomass (right panel) in the upper 50 of the water column in the section shown in Figure 1, between February and September 1995.

DISCUSSION

Life cycle

The spring bloom in the Norwegian Sea appears to be related to the onset of the thermocline in the upper layer (Sverdrup, 1953). In the Atlantic part of the Norwegian Sea this usually happens in May (Aure, 1998; Dale, 1999; Heath *et al*., 2000, Slagstad *et al*., 2000). Thus the presented monitoring in May is close to the onset of the spring bloom in that area. In the area that is covered by the EICW few observation exist that give information on timing of the spring bloom. The presented data show that almost every year during the 1990s the phytoplankton biomass in May was higher in the EICW that in the AW, and data from Gaard and Hansen (1991) and Gaard (1996) from the same section indicate that the spring bloom typically starts earlier in the EICW part than the AW part of the Norwegian Sea. The reason is apparently stronger stratification of the upper layer in the EICW. This stronger stratification in the EICW seems partly to be due to higher temperature gradient in the cold water (Figures 3 and 4) but may also be strengthened by low saline water close to the surface (Gaard and Hansen, 1991; Hansen *et al.*, 1998a). Interannual variability in phytoplankton biomass co-fluctuates well with stratification (Figure 4) and may largely be a consequence of variable weather condition (e.g. wind, solar radiation or air temperature).

Many studies have reported the importance of food availability for egg production of *Calanus finmarchicus* (e.g. Diel and Tande, 1992; Hirche, 1996b and references therein, Hirche *et al*, 1997; Niehoff *et al*., 1999). Although several studies have shown that the peak fecundity of *Calanus finmarchicus* is coupled with the phytoplankton spring bloom, there is a substantial pre-bloom egg production in the Atlantic part of the Norwegian Sea and adjacent Atlantic areas **(**Gislason and Astthorsson, 2000; Niehoff *et al*., 1999, Richardson *et al*., 1999; Gaard, 2000, Niehoff and Hirche, 2000; Hirche *et al*, 2001).

The fact that young *C. finmarchicus* copepodite stages always dominated in the Atlantic Water in May shows that there has been some reproduction in that water for some time prior to the sampling. In average, about 80% of the collected *C. finmarchicus* in the AW were CI, CII and CIII. Having in mind that the mesh size of the plankton nets that were used for the samplings (200 µm) most likely have caused an underestimation of the smallest individuals in the samples (Nichols and Thompson, 1991), and the real concentrations of the smallest copepodites can be expected to have been even higher than indicated in Figures 3, 5 and 7. In addition are the nauplius larvae, which for the same reason are not included into the figures.

Based on the Belehrádec function given by Corkett *et al*. (1986) and Miller and Tande (1993) and the temperature in the area (Heath *et al*., 2000b) it can be calculated that most of these young copepodites in the AW part of the section have been about 3-4 weeks old and the nauplii are produced within the last ~ 20 days. Hence, there has been some egg production in the AW to the north or west of the Faroes for a large part of April. Having in mind that this is the time that overwintered *C. finmarchicus* ascend to the surface layer (Heath, 1999; Gaard and Hansen, 2000; Gislason *et al*., 2000) we must assume that *C. finmarchicus* females in the Atlantic water have had some egg production ever since they have reached the surface. This is also in agreement with egg production measurements on the weather station M in the central Norwegian Sea (66°N, 2°E) which have shown some egg production already in early April (Niehoff *et al*., 1999; Niehoff and Hirche, 2000; Hirche *et al*, 2001) and in the Faroe Shetland Channel in March (Richardson *et al.*, 1999). The recruits found in May on the section are, however, probably not spawned on the locations where they are collected but most likely are advected to the area. Based on satellite-tracked drogue experiments (Hansen *et al*., 1998b) and current measurements in the area (Hansen and Østerhus (2000) the recruits copepodites that are collected on the section (the AW part) in May, may have been spawned to the west of the Faroes or close to the Faroe-Iceland Ridge area, northwest of the Faroes.

In the EICW the stage development is significantly later. In May 1990-2002 average proportion of young copepodite (recruit) stages (CI-CIII) of *C. finmarchicus* represented only about 7% while the remaining 93% were overwintered individuals (CIV-CVI). The presented difference in peak recruitment in the EICW compared to the AW in the Norwegian Sea agrees with other findings. Thórdardóttir *et al.* (1979) found that *C. finmarchicus* in the EICW was dominated by CIV, CV and females in June 1979 while it in the AW further south and east was a mixture of all stages and they concluded that the reproduction in the EICW was at least 1½ month later than in the AW. Also Gaard (1996) concluded that the main recruitment in the EICW apparently is in June.

Due to different timing of reproduction during spring and the different temperature dependent stage duration, they produce two generations per year in the AW while the individuals in the EICW only produce one generation.

Ingestion, maturity and reproduction in May

In despite of much lower phytoplankton concentrations in the AW than in the EICW in May 2002 the *C. finmarchicus* females were physiologically more active in the warm AW the in the cold EICW (Summarised in Table 1). Their feeding activity was in average 1.7 times higher in the AW, the mean proportion of mature females was 1.7 times higher and the mean egg production rate was 1.8 times higher in the AW than in the EICW. Consequently, the mean egg production rate per mature female (those capable of spawning) was roughly the same in both water masses. The higher mean fecundity in AW than EICW seems mainly to be a result of the state of reproductive maturity rather than *in situ* food conditions. This relationship between maturity and mean egg production rates is also shown in earlier observations, on the Scotian Shelf (Runge, 1987), the Labrador Sea (Campbell and Head, 2000), and the southeastern Norwegian Sea (Niehoff and Hirche, 2000).

Based on the abundance of young copepodite stages in May in the two water masses, the reproduction obviously has gone on for the last month in the AW while this apparently not was the case in the EICW. One possible reason for this difference is lower female gonad maturity in the AW than in the EICW. If so, the difference in maturity may have been even higher earlier in spring. The reason for why the females in the AW mature earlier in spring than in the EICW is not known, but it may be connected with ingestion. Moulting and gonad development requires energy, which partly may arise from lipid stores (*e.g*. Jónasdóttir, 1999; Rey-Rassat *et al*., 2002). However, Niehoff *et al*. (1999) demonstrated that gonad maturity increased with food availability during spring in the central Norwegian Sea, and studies by Rey *et al.* (1999) indicate that ingested food may be important to complete the gonad development. Thus, it is possible that higher ingestion rates in the AW (possible due to higher temperature) than in the EICW may be a reason for the higher proportion of mature females (and most likely also earlier maturation during spring) in the AW than in the EICW.

Converting ingestion rates from chlorophyll equivalents to carbon is connected with uncertainties. The conversion factor is variable and depends on *e.g.* phytoplankton species and environmental conditions. Estimating a C/Chl. *a* ratio of 50, the ingestion in the AW and EICW was approximately 4 and 2.3 µgC female^{-1} day^{-1} respectively. Ingestion of heterotrophic microplankton was not measured, but based on measurements by Irigoien *et al*. (1998) on weather station M in spring 1997 it seems to be of minor importance compared to the phytoplankton during spring. The ingestion value shown above can be compared to the energy required for fuelling the measured egg production. Assuming a carbon content of 0.23 µgC egg^{-1} (Oman and Runge, 1994) and a gross growth efficiency of 0.3 (average from Checkley (1980), Berggreen *et al*, (1988), Peterson (1988) and Kiørboe (1989)), the mean egg production rates (Table 1) would require an ingestion rate per female of about 6.4 and 3.6 µg C day^{-1} in the AW and EICW respectively. Thus, the mean ingestion of phytoplankton only covered about 2/3 of the mean carbon requirements. The remaining requirements may e.g. come from a potential heterotrophic contribution, internal lipid stores or a combination of both.

Taking into account that only 70 and 42% of the females in the AW and EICW respectively were capable of spawning, the average egg production rates of these females alone would be 13.3 and 12.4 eggs female^{-1} day^{-1} in the AW and EICW respectively. This would require an ingestion rate per mature (potentially spawning) female of about 9.2 and 8.4 µgC day^{-1}. The ingestion rate values shown in Table 1 are based on all females (mature and immature). It is likely that the actively spawning females may have higher ingestion rates than the immature once. The technique used for gut fluorescence measurements does, however, not allow separation of mature and immature females, and it is therefore not possible to see whether or not the actively spawning females were more actively feeding than the immature females.

Table 1. Mean *in situ* temperature and chlorophyll *a* values and reproductive and ingestion values in the upper 50 m of the water column on 10-11 May 2002 in the AW and EICW respectively on the section shown in Figure 1.

	AW	EICW
Temperature (°C)	7.6	3.8
Chlorophyll a (µg l^{-1})	0.6	2.2
Fecundity (Eggs $female^{-1}$ day^{-1})	9.3	5.2
Total egg production (Eggs m^{-3} day^{-1})	660	643
Maturity (% mature females)	70	42
Egg production per mature female (Eggs $female^{-1}$ day^{-1})	13.1	12.4
Ingestion (ng chl. equiv. $female^{-1}$ day^{-1})	80	46
Ingestion (µg C $female^{-1}$ day^{-1})	4.0	2.3
Calc. carbon ingestion required for egg production (µg C $female^{-1}$ day^{-1})	6.4	3.6

Ocean climate and Calanus finmarchicus

The presented data show that the live cycle as well as the re(production) status of *C. finmarchicus* is quite different in the warm AW and the cold EICW to the north of the Faroes. Variable strength of the East Icelandic Current relative to the Faroe Current affects the ocean climate in the southwestern Norwegian Sea. Such variability is observed between seasons (Hansen and Østerhus, 2000) years (Figure 2) and decades (Blindheim *et al*, 2000). Variability in the area to the North of the Faroes covered by the AW and EICW respectively will highly affect the status of *C. finmarchicus* in the area and consequently also affect the large amounts of pelagic fish that feeds in the area during summer. In extreme cases it may also affect the status of *C. finmarchicus* around the Faroe Islands.

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