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# Mesozooplankton distribution, feeding and reproduction of *Calanus finmarchicus* in the western Norwegian Sea in relation to hydrography and chlorophyll *a* in spring

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## ABSTRACT

Species composition, mesozooplankton distribution, and feeding and reproduction of *Calanus finmarchicus* were investigated in the western Norwegian Sea in May 2003. Copepods were the most numerous group (~85-96% of all the animals caught). *Calanus finmarchicus* (mainly stage CV and females) was the dominant species among the copepods (~42-92%). Among the copepods *Oithona similis* was the second most numerous species (~5-58%). Maximum abundance of *C. finmarchicus* was observed in the southeastern part of the studing area, whereas the lowest abundance of *C. finmarchicus* was observed on the northwest, where cold water from the East Icelandic Current enters the Norwegian Sea. Gut content of *Calanus finmarchicus* females varied from 0.78 to 10.73 Chl *a* equiv. ng female$^{-1}$. The proportion of mature females (GS4) varied between 41 and 98%. The highest proportion of mature females was observed in the Atlantic water in the northeast. On average about ~43% of the females were spawning. Daily rates of egg production varied from low (1 egg female$^{-1}$ d$^{-1}$) to high (101 eggs female$^{-1}$ d$^{-1}$). Mean egg production was 16 eggs female$^{-1}$ d$^{-1}$. No statistically significant relationship was found between egg production of *C. finmarchicus* and temperature, chlorophyll *a* concentration, females gut content, prosome length and weight. In cold Arctic water feeding and reproduction activity of *C. finmarchicus* population was higher, whereas abundance of zooplankton was higher in warmer Atlantic water.

*Keywords: zooplankton abundance, Calanus finmarchicus, Norwegian Sea, gut content, gonad stage, egg production.*

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# 1 INTRODUCTION

It's well known that *Calanus finmarchicus* (Gunnerus) is one of the dominant species of the northern seas in terms of abundance and biomass (Wiborg 1955, Marshall and Orr 1972, Gislason and Astthorsson O.S. 1996, Irigoien *et al*. 1998, Melle and Skjoldal 1998, Irigoien *et al*. 2000, Hirche *et al*. 2001, Pasternak *et al.* 2002). The Norwegian Sea is one of the areas, where this species is found in great abundance (Colebrook 1982, Planque *et al*. 1997).

*C. finmarchicus* is mainly an herbivorous species and plays an important role in transferring primary production to the higher tropic levels in the food web (Mauchline 1998). In the Norwegian Sea, *C. finmarchicus* is an important prey for commercial pelagic fish such as herring, mackerel and blue-whiting. It has been hypothesized that the predator-prey relationship between herring and *C. finmarchicus* may affect important life history characteristics of *C. finmarchicus*, such as the time of spawning, annual ascent and descent and the number of generations per year (Kaartvedt 1996, Kaartvedt 2000). It has further been hypothesized that herring may adapt its feeding migrations pattern according to the annual development of *Calanus* (Corten 2000, Kaartvedt 2000). After spawning, herring mainly feeds on pre-spawning concentrations of *C. finmarchicus*, and therefore when studying the feeding migrations of herring, it is important also to study the age structure of *C. finmarchicus* (Shaposhnikova 1964, Melle *et al*. 1994, Dalpadado *et al*. 2000).

Reproduction is an important process in population dynamics (Carlotti and Hirche 1997). A number of studies, both experimental and field ones, on *C. finmarchicus* egg production have been carried out. They have shown that egg production depends on both maternal factors, (e.g. size of females and gonad stage) and environmental conditions, (e.g. ability of food and temperature) (Melle and Skjoldal 1989, Prestidge *et al.* 1995, Hirche 1996, Rudge and Plourde 1996, Carlotti and Hirche 1997, Hirche H.J. *et al*. 1997, Campbell and Head 2000b, Gislason and Astthorsson 2000, Niehoff and Hirche 2000, Mayzaud P. *et al.* 2002, Durbin *et al.* 2003). These studies have been carried out in several different areas in various parts of the North Atlantic. However no previous investigation on egg production has been carried out in the western Norwegian Sea.

Annual and inter-annual changes in physical conditions of the sea affect the production of phytoplankton and life history of copepods. Feeding, gonad maturation and egg production play an important role in adaptation of *C. finmarchicus* to such a changeable environment conditions (Niehoff *et all* 1999) and knowledge of production characteristics of *Calanus* may help to assess more accurately secondary production (Hirche 1990).

As *C. finmarchicus* is mainly herbivorous, its reproduction and development depends on quality and quantity of phytoplankton. Several authors (Runge 1985, Hirche 1990, Smith 1990, Hirche and Kattner 1993, Campbell and Head 2000a) have found that *Calanus* reproduction is related to the available food. In this context the onset of spring phytoplankton blooming is an important event. Several studies have shown that not only diatoms are food source for *C. finmarchicus*, but also other microplankton (e.g. Ohman and Runge 1994, Nejstgaard *et al*. 1997, Harris *et al*. 2000). The

availability of lipid reserves is a major source for gonad maturation of *Calanus* in early spring (Jónasdóttir 1999).

The aim of this study is to describe zooplankton community structure, and investigate gonad development, egg production and feeding of *C. finmarchicus* in relation to phytoplankton production and hydrographic conditions in the western Norwegian Sea. The western part of the Norwegian Sea is an interesting area for investigation of the life strategy of *C. finmarchicus* (its reproduction, and feeding) for to several reasons. Firstly, in the area two currents of different characteristics (cold Eastern Icelandic Current and warm Atlantic Current) meet. Also, there are changes in the dominant species in this area where the boreal *C. finmarchicus* is being replaced by the larger arctic *C. hyperboreus*. Finally, planktivorous fish such as herring, mackerel and blue-whiting undertake their feeding migrations to the area. As stated above these feeding migrations may affect on the population dynamics of *C. finmarchicus* (Dalpadado *et al*. 1996, Corten 2000, Kaartvedt 2000).

Another reason for choosing this topic is the possibility of learning new techniques and methods in zooplankton work that can be applied to plankton investigations in the Polar Research Institute, Murmansk. The study is a part of a cooperative research program of the Marine Research Institute, the Institute of Marine Research, Faros Fisheries Laboratory and the EU on the herring migrations in the Norwegian Sea (Misund *et al*. 1998). Obtained data will be added to the database of the Marine Research Institute.

## 2 LITERATURE REVIEW

In the western part of the Norwegian Sea water masses of different origin interact (cold East-Icelandic Current in the northwest and warm North-Atlantic Current in the south and east).

In the Norwegian Sea, longitudinal and latitudinal variations of phytoplankton development have been observed (Niehoff *et al*. 1999). In the open part of the Norwegian Sea the spring phytoplankton blooming starts, when the water column becomes stratified. The reason is that warming of surface water taken a longer time if it was only fresh water flow made the stratification. Therefore, pre-bloom period is prolonged and phytoplankton develops later and continues longer. The long blooming period gives zooplankton organisms a chance to become mature and to develop new generation during a period with good feeding conditions (Dale *et all*. 1999).

In the zooplankton community of the Norwegian Sea, copepods are the dominant group. Among the copepods, *C. finmarchicus* is the most important species in terms of abundance and biomass (Abramova 1956, Astthorsson *et al.* 1983, Mauchline 1998, Heath and Jónasdóttir 1999, Irigoien *et al.* 2000, Green *et al*. 2003). In the cold water of the East Icelandic Current the dominance of *C. finmarchicus* is somewhat decreased mainly due to increasing of abundance of the bigger cold water species *C. hyperboreus* and *Metridia longa* (Astthorsson *et al*. 1983, Astthorsson and Gislason 1995). *Oithona similis* is a common and numerous copepod species in northern waters (Wiborg 1995), but due to its small size it doesn't play a prominent role in terms of biomass in the zooplankton community. Carnivorous chaetognaths (*Sagitta spp.*,

*Eukrohnia spp.*) are also abundant in the Norwegian Sea, but they are most abundant in really deep water, and occurring mostly below a depth of 100 m. Other zooplankton species or taxonomic groups are less important in the area (Wiborg 1995, Astthorsson *et al.* 1983).

Under certain conditions grazing by copepod may be a more important factor in the reduction of phytoplankton biomass than lack of nutrients (Colebrook 1982). Several investigations on feeding habits of *Calanus* species have been done in different areas (e.g. Marshall and Orr 1972, Mackas and Bohrer 1976, Boyd and Smith 1980, Dagg 1983, Ellis and Small 1989). As summarized by Boyd and Smith (1980), the quantity of chlorophyll and its degradation products in copepod guts reflects the quantity of phytoplankton consumed and should correlate to grazing rates of phytoplankton. In the field, the gut content of copepods may vary considerably over depth as well as between day and night, and duel variations in feeding have been shown to be closely related to diel migrations of copepods (Mackas and Bohrer 1976). Dagg (1983) pointed out that changes of gut fullness may show changes in copepod feeding activity and concentration of food.

After diapauses at the end of winter, *C. finmarchicus* ascend to the surface for reproduction. According to Plourde and Runge (1993), *C. finmarchicus* needs high food densities to begin producing eggs. Therefore maximum egg lying should thus occur just after the spring bloom (Marshall and Orr 1972). Fed *Calanus* mature more quickly and lay more eggs than it starved (Marshall and Orr 1972). Data by Dale *et al.* (2001) also indicate that egg production depends on phytoplankton biomass, being low, under post-bloom conditions and high under the bloom conditions. However, there are a number of studies, where the opposite pattern is shown. Thus, Melle and Skjoldal (1989) pointed out that the presence of spawning *C. finmarchicus* females and individuals on copepod stage V before the spring bloom may reflect that reproduction occurs before the bloom. Richardson *et al*. (1999) hypothesized that even a limited pre-blooming period may be important for *Calanus* population. Hirche *et al.* (2001) wrote that *C. finmarchicus* females laid half of their eggs before the bloom. They noted that the eggs spawned before the bloom could develop into feeding applier stages and some even into copepod stages CI and CII. However, most of copepodites seemed to die off from the population at these stages (CI and CII) and recruitment to the older stages was not observed during the pre-bloom period (Hirche *et al.* 2001). According to Diel and Tande (1992), advanced maturation of females and egg lying before the bloom may be viewed as an adaptation towards utilizing the whole growth period of the phytoplankton.

Gonad maturation and reproductive rate are important parameters in population dynamics (Hirche *et al.* 1997, Niehoff *et al.* 1999). It is still not known if biological mechanisms or environmental conditions are more important for *C. finmarchicus* egg production (Hirche *et al.* 1997). As described by Marshall and Orr (1972), *C. finmarchicus* produce eggs in a series of bursts or clutches, each lasting about a week. The egg production rate is determined by clutch size and clutch deposition interval (Hirche *et al.* 1997). Environmental conditions such as temperature, availability of food and its quality and quantity, previous feeding as well as female size and gonad stage may influence reproduction state of *C. finmarchicus* (Hirche 1990, Diel and Tande 1992, Jónasdóttir 1994, Campbell and Head 2000a).

Laboratory experiments show that egg production increases with higher food concentration (Hirche *et al*. 1997). The experiments show that the quantity of food is a limiting factor for egg production, at least before the bloom (Niehoff *et al.* 1999). Marshall and Orr (1972) reported that females of *C. finmarchicus* produced different numbers of eggs by feeding on different forms of phytoplankton, and Lacoste *et al*. (2001) found that fecundity, egg laying and hatching were affected by phytoplankton species combination. Several other factors such as female age, reduction of male fertilization capacity caused by consumption of certain din flagellates species may reduce *Calanus* reproduction (Ianora *et al.* 1999). There are some studies for different copepod species that show that low egg production and high level of applier mortality as well as abnormal development of eggs and applier may be caused by high diatom concentrations (Poulet *et al*. 1995, Uye 1996).

Several workers have observed significant correlation between egg production rate and chlorophyll *a* concentration in the field (Runge 1985, Hirche 1990, Smith 1990, Melle and Skjoldal 1998). Niehoff *et al.* 1999) found that egg production rate and clutch size of females were significantly related to chlorophyll *a* concentration at the time of phytoplankton blooming. However, Melle and Skjoldal (1989) and Niehoff *et al.* (1999) found that spawning of *C. funmarchicus* starts before to the onset of spring phytoplankton blooming. There are also reports (Plourde and Runge 1993, Ohman and Runge 1994, Dale *et al.* 2001) where no significant relationship was found between phytoplankton stock and *C. finmarchicus* egg production rate). Diel and Tande (1992) observed that egg production began prior to increase of phytoplankton. However, the final female maturation is finished at the beginning of spring bloom (Diel and Tande 1992).

In high latitudes, offshore thermal stratification of the water column is a prerequisite for spring phytoplankton blooming (Diel and Tande 1992) and temperature may play an important role in the process of *C. finmarchicus* maturation and its reproduction. Plourde and Runge (1993) found that colder temperature in the beginning of spring would delay the spring bloom and the onset of egg production of *C. finmarchicus*. Runge (1985), Hirche *et al.* (1997) and Campbell and Head (2000a) pointed out that egg production rates increased with increasing temperatures.

According to Hirche *et al.* (1997) there is also endogenous control of egg production (i.e. lipid reserves) as maximum egg production was less than expected at optimum temperature and feeding conditions. Irigoien *et al*. (1998) marked that egg production of *C. finmarchicus* females depends more on internal lipid source than on food, after they have migrated to the surface after winter diapauses.

Hirche (1990) reported that egg production of females of *C. finmarchicus* was related to female weight, but not to presume length. However, Campbell and Head (2000a) found a significant correlation between clutch sizes and presume length of *Calanus* females. Runge (1985) noted that both body size and ambient temperature may influence maximum egg production rates.

Early copepod stages of *C. finmarchicus* accumulate lipids in the oil sac, whereas the mature females utilize the content of the oil sac (Marshall and Orr 1972). The lipids stored in the oil sac of the females play a role in formation of eggs and at least allows the female to build organic in the ovary (Carlotti and Hirche 1997). Thus, females can

easily produce eggs even without food. But the length of over wintering period and losses of body reserves due to starvation in spring may affect maturation time. Diel and Tande (1992) marked that spawning of *Calanus* before spring phytoplankton bloom seems to be an advanced mechanism of regulating its maturation. Hirch and Kattner (1993) found that starved females could utilize their lipid reserves to produce eggs with high hatching rates. Ohman and Hirche (2001) pointed out that *C. finmarchicus* females used lipid reserves and nutrition from micro plankton for gonad maturation. Irigoien *et al.* (1998) suggested that *Calanus* females used their lipids for reproduction when ingestion of phytoplankton was insufficient for building eggs.

Adult individuals of *C. finmarchicus*, particularly females, are prey for planktivorous fish (Dalpadado *et al.* 1996). Thus, the reproduction is a potentially risky process for *Calanus*. Consequently, spawning prior to the start of fish feeding migration seems to be beneficial for *Calanus*. Kaardtvedt (2000) hypothesized that pre-bloom spawning of *C. finmarchicus* may minimize the risk of an encounter with planktivorous fish during their seasonal feeding migrations of the fish.

# 3 MATERIAL AND METHODS

## 3.1 Sampling

Sampling was carried out in the western part of the Norwegian Sea between 14 and 30 May 2003 (Figure 1).

Temperature and salinity were recorded with a CTD (Sea Bird Electronics SBE-9) at 35 stations. Seawater samples for measurement of chlorophyll *a* were collected at 20 stations from depth of 10 and 30 m. The seawater samples were filtered through GF/C glass fiber filter on board the ship. At the laboratory onshore the filters were homogenized in 90% aqueous acetone and the extract measured in a spectrophotometer according to the method described by Strickland and Parson (1968).

Zooplankton data was collected at 13 stations using a WP-2 net (0.25 $m^2$ mouth opening, 200 µm mesh size) by vertical hauls (towing speed was ~1 m $s^{-1}$) from 100 m to the surface. The volume of water filtered by the net was measured with a flow meter. On each station two plankton hauls were made. One sample was preserved in 4% neutralized formalin and used for analysis of abundance and species composition of zooplankton and gonad stage of *C. finmarchicus* in the laboratory onshore. The other sample was taken to collect live *C. finmarchicus* females to measure egg production by incubation experiments on board the ship.

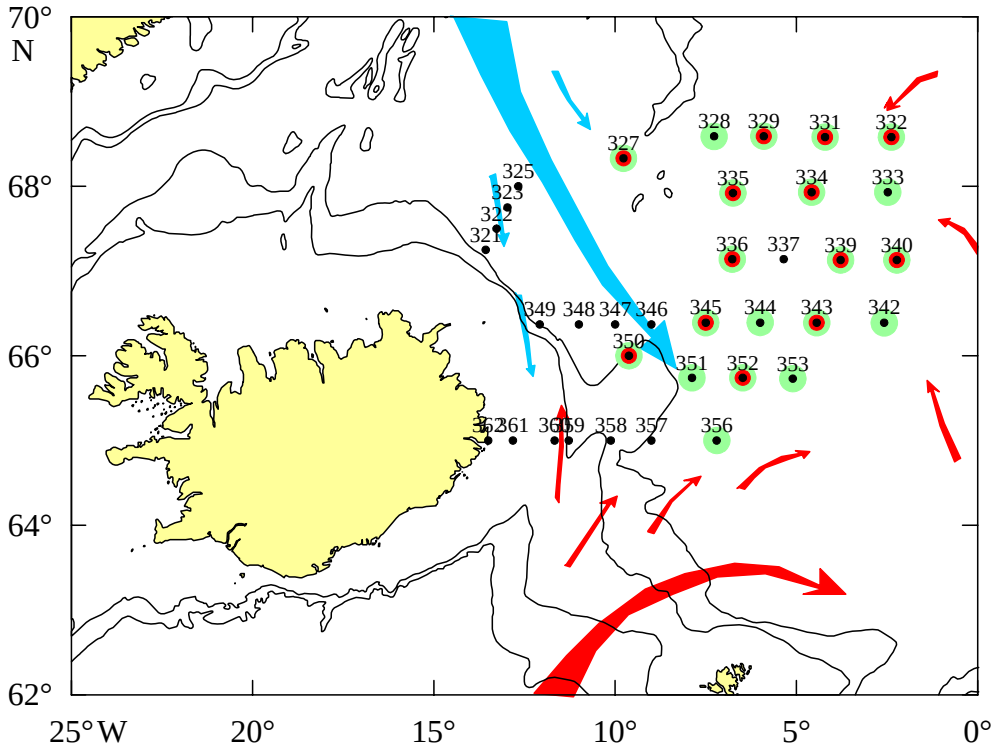



**Figure 1: Location of the sampling stations in the western part of the Norwegian Sea (black dots – hydrograph Stns, red dots – plankton Stns, green dots – phytoplankton Stns). The number above the circles is indicates station number. The 500 and 1 000 m depth contours are also shown. Red arrows indicated flow of the warm Atlantic water. Blue the cold East Icelandic water (Hansen and Østerhus 2000).**

The samples for *C. finmarchicus* eggs production were taken with a WP-2 net fitted with a non-filtering cod-end. The net was towed slowly (~ 0.3 m $sec^{-1}$) and after the net arrived on the deck the cod-end was removed immediately from the net. The content of the cod-end was gently emptied into a ~15 liter bucket containing water. Healthy females were picked out from the sample and put into egg production chambers (65 cm diameter, 180 mm height). One female was added to each chamber and at each station 20 replicates were done. 20 females from each sample were placed into individual egg production chambers for 24 hours in a dark at ambient seawater temperature. The chambers were equipped with nets (330 µm mesh size) for separating eggs and females to prevent *C. finmarchicus* cannibalism as females may eat their own eggs (Runge and Plourde 1996). The eggs were filtered onto a 20-µm screen, on which they were counted immediately under a stereomicroscope. After egg counting, the females of *Calanus* were preserved in 4% neutralized formalin. In the laboratory onshore the presume length of the females was measured.

The rest of the animals from the live samples were filtered through a small piece of net, packed in plastic bags (10x10 cm) and frozen in a freezer (-20°C) immediately after sampling. In the laboratory onshore, 30 females were picked out from each sample for gut fluorescence analysis.

For some of the analyses the data has been divided into those collected in warm Atlantic Water (T>3.5°C, S>34.9 psu; Stns 329, 331, 332, 334, 335, 336, 339, 340, 343, 352) and those collected in cold Arctic Water (T<3.5, S<34.9; Stns 327, 350, 345)

## 3.2 Sample processing

### *3.2.1 Zooplankton enumeration and species identification*

Larger zooplankton organisms (euphausiids, chaetognats, amphipods, mysids, and decapods) were counted and length measured from the whole samples. For enumeration and measurements of other animals subsamples were used, using a Motoda splitter (Motoda 1959). The subsample contained at least 400-500 individuals for quantitative analyses. All the individuals in the sub sample were determined to species and counted. Some of the copepods (*Metridia longa*, *Pareuchaeta Norwegian* and *Pseudocalanus elongates*) were classified into copepod stage groups (I-III and IV-V). *C. finmarchicus* and *C. hyperborean* (Kröyer) were classed to copepod stages from an aliquot containing at least 200 individuals.

Nauplii found in the samples were in the size range between 0.2 and 0.6 mm. Based on this they were all determined as *C. finmarchicus* nauplii. The eggs were separated in two groups according to their size and the smaller eggs (~0.16 mm) we determined as *C. finmarchicus* while the bigger ones (0.32-0.38 mm) were classed as “other copepod eggs”.

### 3.2.2 *Gut fluorescence*

Gut fluorescence determination gives information about quantity of algal pigments (amount of gut content). The analysis is based on pigment extraction from organic solvent (Båmstedt *et al.* 2000).

A small piece of the frozen sample was placed into a Petri dish for thawing. The chlorophyll is quickly degraded by light to phaeopigments (Mackas and Bohrer 1976) and therefore the sample was kept in a dark place while thawing. Ten female *C. finmarchicus* were picked out from each sample. When sorting, the animals were carefully handled so that female bodies were not injured. Three replicate samples were done for each sample. The sample were put into 5 ml tubes containing 90% acetone at 4°C and kept in a refrigerator until next day. All the tubes were covered with Para film to avoid evaporation of acetone.
Content of chlorophyll *a* was measured by standard fluorometric procedure (Mackas and Bohrer 1976). The fluorescence of the extract was measured by a Turner Designs Fluorometer (10-AU). After measurement of the fluorescence, 3 drops of 10% HCl were added and after 1 minute the fluorescence was measured again.
Gut pigments amount was calculated using the following equations (Ellis and Small 1989), modified from Strickland and Parsons (1968):

Chl *a* = C (R/R-1) ($F_o$-$F_a$)(v/n)

Pheopigment = C (R/R-1) (R (Fo-$F_a$) (v/n)
C – Fluorometer calibration constant
$F_o$ and $F_a$ – the fluorescence reading before and after acidification
R – The acidification ratio (2, 27)
v – The extract volume (5 ml)
n – The number of individuals in a tube (10 and.)

The Fluorometer was calibrated according to the following procedure. Standard samples from ampulla's chlorophyll *a* were made. The sample was diluted with 90% acetone and samples of different concentration (0.022, 0.11, 0.22, 1.1, 2.2, 5.5, 11 µg Chl *a* $l^{-1}$) were measured. The measurement of the standards was made the same way as for animals. Three drops of 10% HCl were added and after mixing it was measured again.

Fluorometer calibration constant (C) was found from linear regression of the standard line (fluorescence reading of known concentration, made from the chl. *a* ampulla's). In our case calibration constant was equal 0.3089 µg Chl *a* $l^{-1}$ (Figure 2).

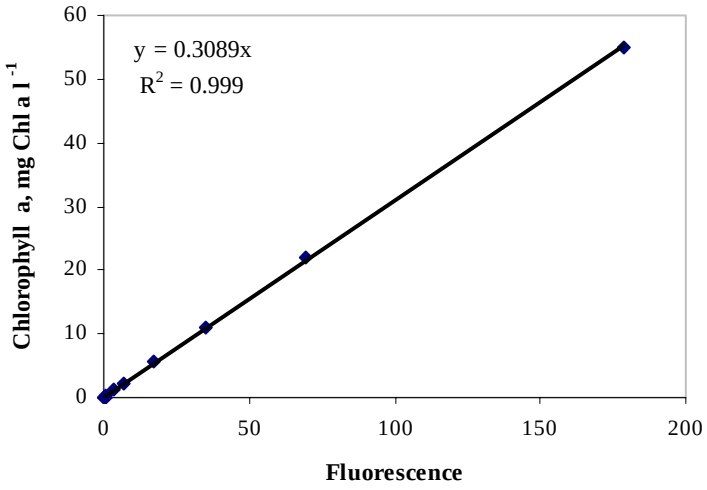



**Figure 2: The calibration curve. Fluorescence values plotted against chlorophyll *a*. Equation of linear regression and determination coefficient are shown on the plot**

The gut content in unites of chlorophyll *a* equivalents per individuals (ng Chl. *a* equiv. $ind.^{-1}$) was calculated as:

G = (Chl *a* + 1.51 * Pheopigment)

### 3.2.3 *Gonad stage determination*

From each formalin preserved sample 30-50 female of *C. finmarchicus* were picked out for gonad stage determination. The gonads of *C. finmarchicus* were stained according to a modified method of Niehoff and Hirche (1996). The females were stained with 2% borax carmine in methyalcohol for 12 h. Then the females were put in 50% ethanol with 0.5% HCl for 24 h. After that the females were dehydrated in an ethanol series – 50% for 1 h, 70% for 2 h, 90% for 2 h, and 95% for 2h. After dehydration the females were put in glycerin for a minimum of 24 h to clear the tissue and to store the animals before determining gonad stages.

The gonad maturity was determined according the system proposed by Niehoff and Hirche (1996) and Niehoff and Runge (2003) with amendments accepted for MRI (Table 1).

**Table 1: The system of gonad maturity stage (GS) classification for *Calanus finmarchicus* females (Niehoff and Hirche 1996 with amendments accepted for MRI)**

| Stage/group | Description of the group |
|---|---|
| GS1 | Only ovary visible, diverticula's empty, oviducts empty or with one row of dispersed small dark red oocytes |
| GS2 | Single row of small dark red stained oocytes visible in diverticula's and oviducts. Can be two rows of small acolytes dispersed in oviduct |
| GS3 | Several rows of small dark red acolytes in diverticula's and oviducts, oocytes increased in size in ventral direction. Ovary and diverticula bigger |
| GS4 | Several rows of small dark red oocytes in the dorsally located part of the diverticula and the oviduct, ventrally large pink oocytes irregular shape visible in one or rows extending throughout the length of the gonad. Big oocytes form the sacs in the oviducts |
| Spent | The diverticula are almost empty. Several big oocytes visible in oviducts |
| Unidentified | Destroyed animals or the females difficult to classify to any stages |

Females of gonad stage (GS) 1-3 are immature while females of stage GS4 are mature and ready to spawn.

### *3.2.4 Presume length measurement*

The presume length and the total length of *C. finmarchicus* females were measured to analyze the correlation between length and the egg production of the females. Formalin preserved females, that had been used in the egg production experiments, were stored in the refrigerator (~4°) until they were measured. All the females were measured using a stereo-microscope (x25). A total of 253 females of *C. finmarchicus* were measured.

### *3.2.5 Weight determination*

The individual weighing was carried out only for *C. finmarchicus* females from the egg production experiments. The animals were weighed individually on a "Cahn" C-31 Microbalance (precision 0.1 µg).

After length measurements, all the females were put individually in previously weighed and numbered small pieces of aluminum foil. The aluminum cups were then put into an oven at 60°C for drying for 48 hours. After drying they were kept in desiccators for half an hour before weighing. A total of 253 females of *C. finmarchicus* were weighed. No correction due to formalin preservation was made.

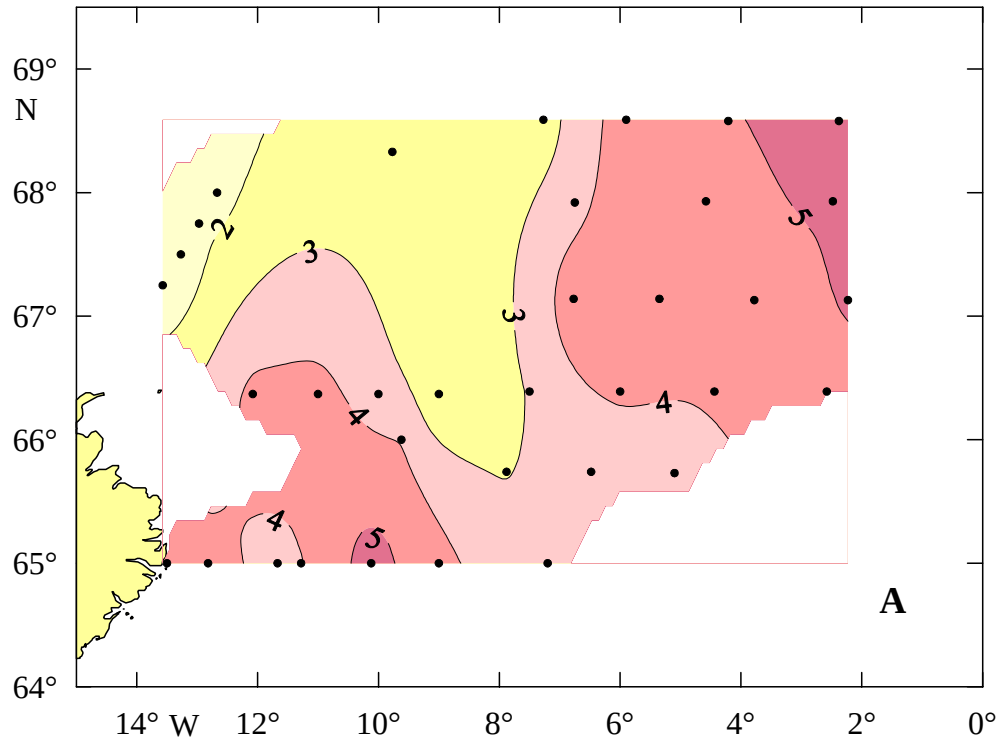
# 4 RESULTS

## 4.1 Temperature and salinity

The study area is influenced by cold and warm water – the cold East Icelandic Current (Arctic water) coming from the northwest and the warm Atlantic Current (Atlantic water) from the south and the northeast.

The distribution of temperature at 50 m is presented on Figure 3A. The temperature varied between 1.2 and 5.8°C. The temperature gradually decreased from the south and east (~4-5°C) to northwest (~5°C) (Figure 3A). The temperature gradient showed a penetration of cold water of the East Icelandic Current from the northwest.

Salinity tended to be lower in the northwestern part of the study area reflecting the influence of the cold East Icelandic Current coming from the northwest (Figure 3B). Highest salinity values were observed in the northeastern part, reflecting influx of Atlantic Water from that direction (Figure 3B).



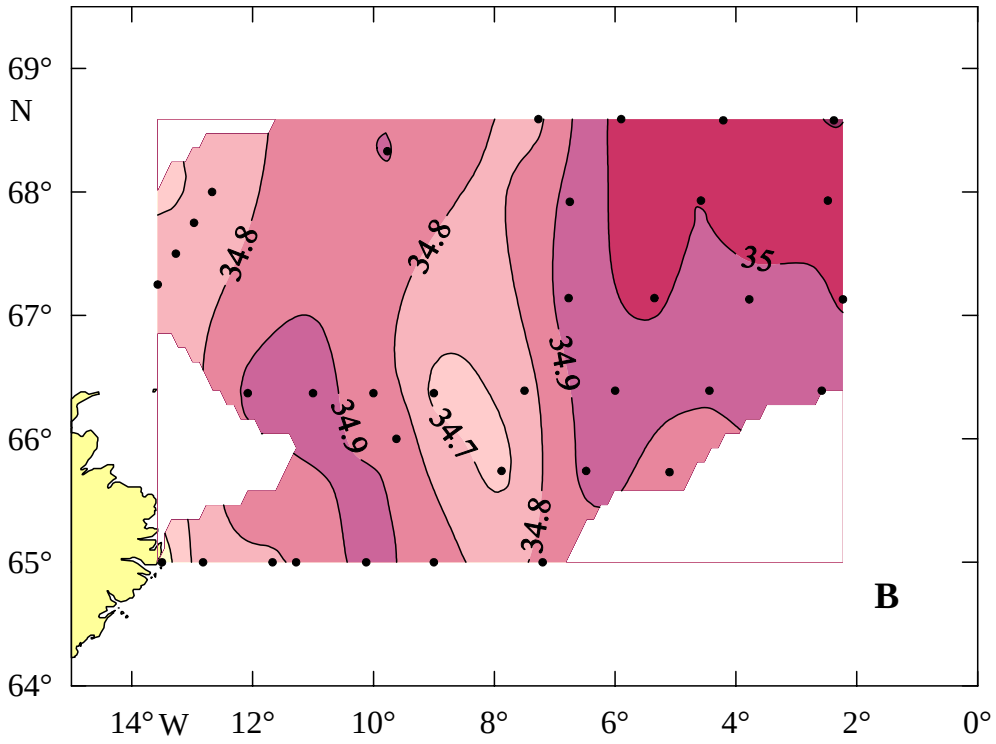



**Figure 3: Distribution of temperature (°C) (A) and salinity (psu) (B) at 50 m depth in the western Norwegian Sea between 22 and 29 May 2003. The dots show the location of the hydrograph stations.**

## 4.2 Chlorophyll *a*

Distribution of chlorophyll *a* concentration is presented in Figure 4. The concentration of chlorophyll *a* varied from ~0.3 to ~6 µg $l^{-1}$. The highest concentration of chlorophyll *a* (~6 µg $l^{-1}$) was recorded in the southwestern part of the study area (St. 350) in Arctic water. The least concentrations of chlorophyll *a* (~0.5 µg $l^{-1}$) were observed in the southern-central part of the study area.

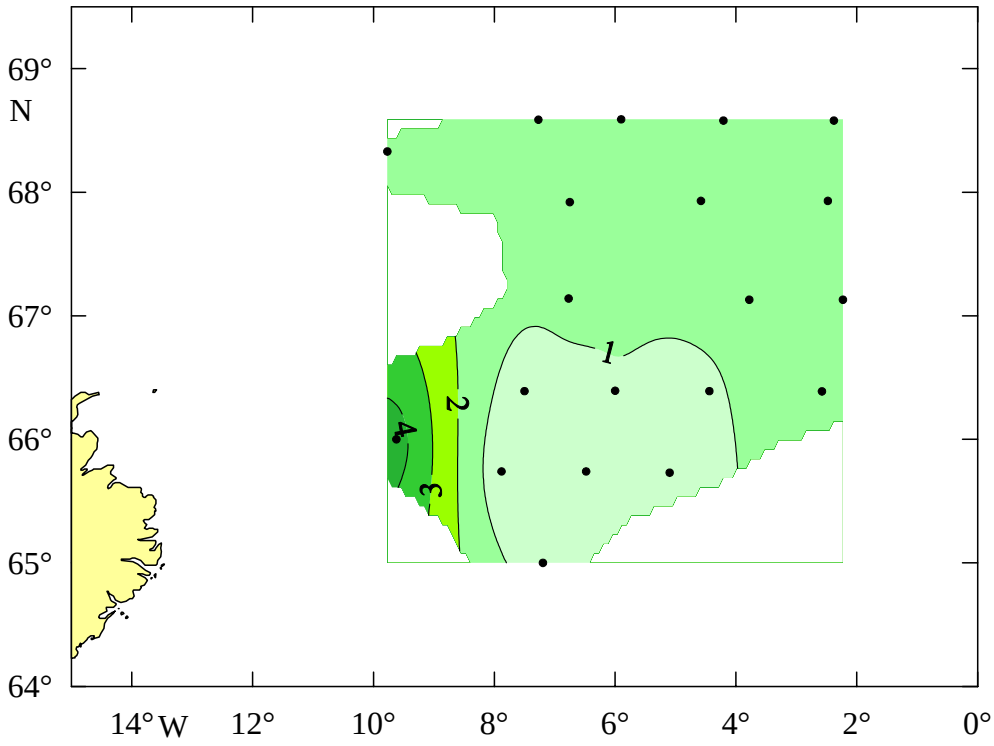



**Figure 4: Chlorophyll a concentration (µg $l^{-1}$) (average values from 10 and 30 m depth) in the western Norwegian Sea between 22 and 29 May 2003. The dots show the location of stations where the chlorophyll *a* concentration was measured.**

### 4.3 Species composition and abundance of mesozooplankton

The abundance of zooplankton was lowest in the northwest (~17 000 and. $m^{-2}$, Stn 327) and highest in the southeast (~123 000 and. $m^{-2}$, Stn 343; Figure 5).

Copepods were the most numerous group in the samples. Approximately 85-96% of all the animals caught were copepods (Figure 5).

Among the copepods, *Calanus finmarchicus* was the dominant species (42-92%) of all the copepods found in the samples (Figure 5). The proportion of *C. finmarchicus* was lower at the westernmost stations (34-16%), where the small cyclopoid *Oithona similes* dominated (55-44%). For the whole area, *O. similes* were the second most numerous copepod species (~5-58%) of the copepods (Figure 5). Eggs of copepods were found at almost all stations but on average their proportion was only ~0.3%. The highest abundance of copepod eggs was observed in the southeast.

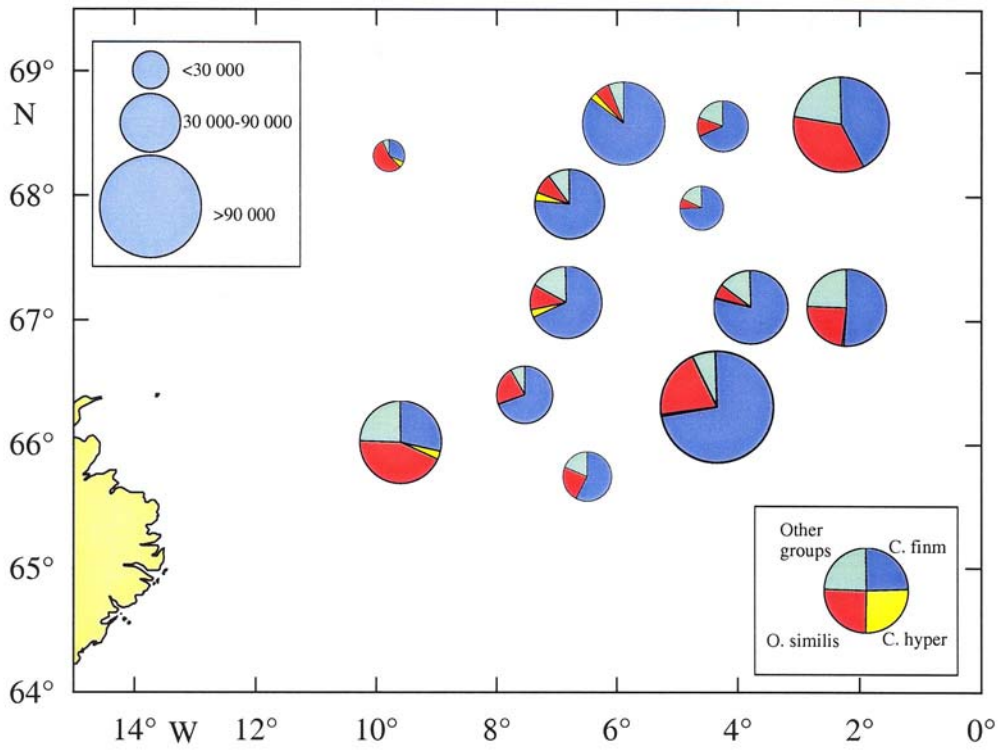



**Figure 5: Abundance (and. $m^{-2}$) and relative composition (%) of zooplankton species in the western Norwegian Sea in the upper 100 m layer between 14 and 30 May 2003.**

Other zooplankter included juvenile periods (*Limacina retroversion*), juveniles and adult chaetognaths (*Eucrohnia spp., Sagitta spp.*) and juvenile hyperiids (*Parathemisto abissorum*). A few individuals of the period *Clione limacine* were observed in the northeastern part of the area. Euphausiid larvae were found regularly in the samples, but adult animals were observed only rarely. Juveniles and adult ostracods (*Conchoecia borealis*) were found occasionally. Young chaetognaths were the most numerous among the non-copepod forms. They were found on every station and their abundance was highest in the southern-central part of the area and in the northeast.

### 4.4 Abundance and age structure of *Calanus finmarchicus*

The abundance of *C. finmarchicus* varied from ~5 400 to ~80 000 and. $m^{-2}$. Highest abundance of *C. finmarchicus* was observed in northern part of the area (Stn. 329; Figure 6) and in the southeast (Stn 343; Figure 6) while lowest abundance of *C. finmarchicus* (~5 300 and 9 400 and. $m^{-2}$) was observed in the western part of the studied area (Stn. 327 and 350; Figure 6), where cold waters of the East-Icelandic enter to the Norwegian Sea.

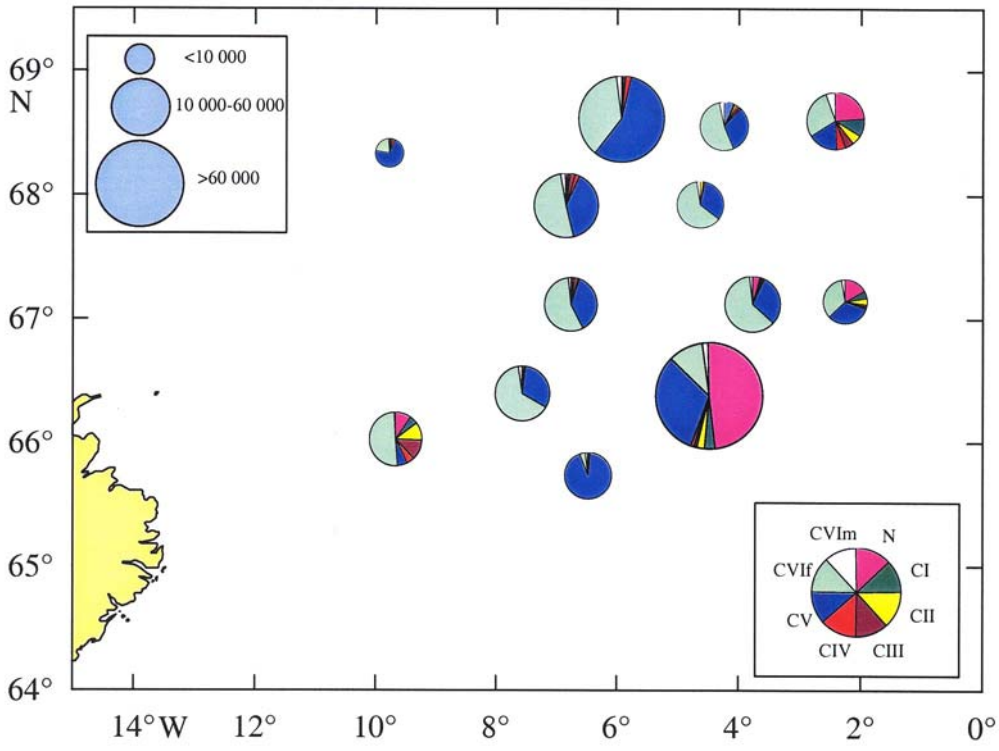



**Figure 6: Abundance (and. $m^{-2}$) and relative composition (%) of copepod stages of *Calanus finmarchicus* in the western Norwegian Sea in the upper 100 m layer between 14 and 30 May 2003.**

The most abundant stages in the *Calanus* population were individuals on copepod stage V and females. Abundance of copepod stage V varied from ~1 300 to ~45 700 and. $m^{-2}$ and female abundance varied between ~1 000 and. $m^{-2}$ and ~31 500 and. $m^{-2}$. Stage CV and females of *Calanus* were most numerous in the northern (~45 700 and ~30 000 and. $m^{-2}$, Stun 329) part of the area. In the northwest (Stn 327) most of the animals were at stage CV (~71%) and females (21%), whereas in the southwest (Stn 350) all development stages were found, females dominated (~51%) and the proportion of copepodites at stage CII and CIII was highest in the study area (~25 and 27% respectively) (Figure 6). The proportion of males was very low in the whole area and did not exceed 6%. Eggs of *C. finmarchicus* were only observed in the southeast and were few in numbers. In the same area the highest abundance of nauplii was observed.

### 4.5 Gut content of Calanus finmarchicus

Average gut content of *Calanus finmarchicus* (Figure 7) varied from 0.8 to 10.7 Chl *an* equiv. ng $female^{-1}$.

Highest level of gut content was observed in southwest part at the same station (Stn 350) where chlorophyll *a* concentration was also highest (Figure 4). There was a significant relationship between gut content and chlorophyll *a* concentration (linear regression, $R^2$=0.88, p<0.001), however the significance was mainly by due to one station (Stn 350). When the analysis was carried out without the data from this station, the relationship was insignificant ($R^2$=0.21, p=0.19).

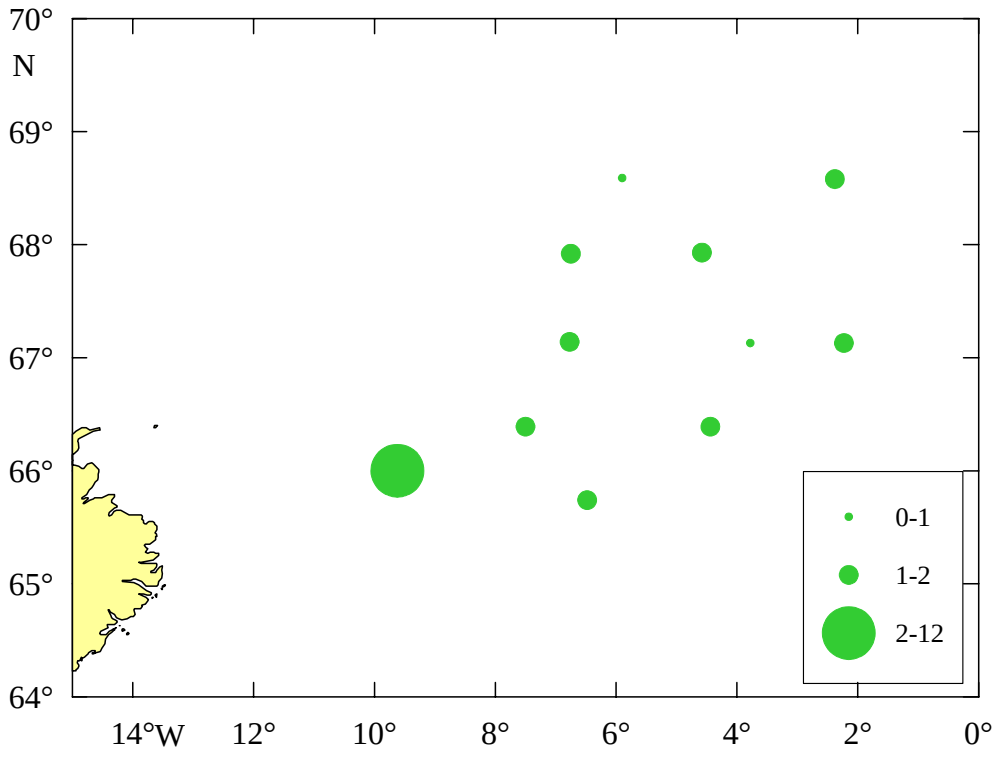



**Figure 7: Average gut content (ng Chl *an* equiv. female$^{-1}$) of *Calanus finmarchicus* females in the western Norwegian Sea between 14 and 30 May 2003.**

## 4.6 Gonad stage of Calanus finmarchicus

Females with gonads in different stages of maturation were found in the samples. The proportion of mature females (GS4) varied between 41 and 98% (Figure 8). The highest proportion of females in GS4 was observed in the southwest (Stn 350) on the northeast (Stns 332, 340, 343). Females in GS 1-3 contributed on average 6-9% of all the females. At two stations in the northeast (Stns 334 and 339) spent females were observed (13 to 33%) (Figure 8).

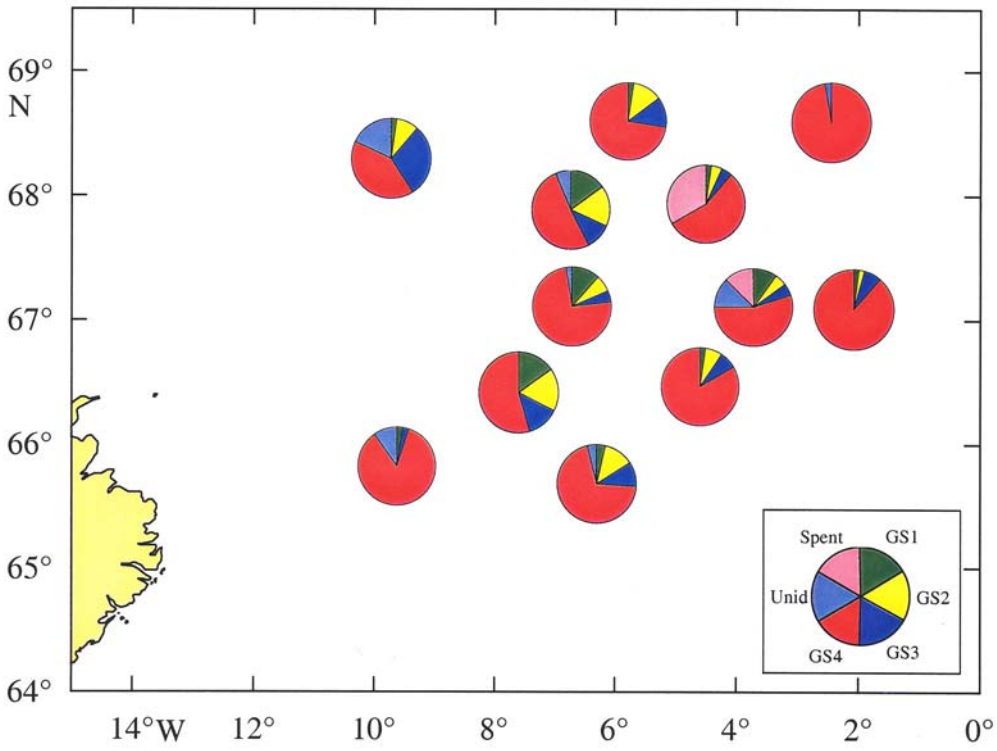



**Figure 8: Relative frequency of gonad development stages of female *Calanus finmarchicus* in the western Norwegian Sea between 23 and 27 May 2003.**

## 4.7 Egg production rate of *Calanus finmarchicus*

On average 43% of the females from egg production experiment were observed to spawn in the egg production experiments. Egg production rates of *C. finmarchicus* females is shown in Figure 9. Daily rates of egg production varied greatly from low (1 egg female$^{-1}$ d$^{-1}$) to high (102 eggs female$^{-1}$ d$^{-1}$). Mean egg production was 16 eggs female$^{-1}$ d$^{-1}$. The highest egg production was observed in the southwestern part of the study area (Stn 350) (44 eggs female$^{-1}$ d$^{-1}$).

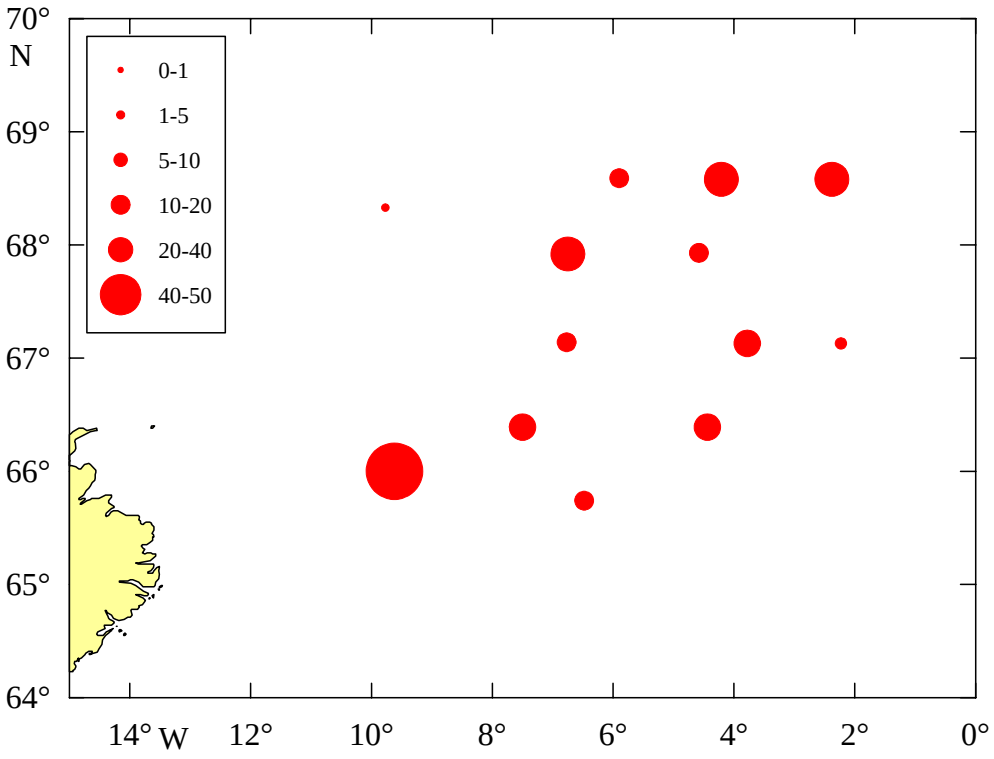



**Figure 9: Egg production rates of *Calanus finmarchicus* (eggs female$^{-1}$ d$^{-1}$) in the western Norwegian Sea between 23 and 27 May 2003.**

## 4.8 Effect of temperature, chlorophyll *a*, gut content, and maternal length and weight on egg production rates of *Calanus finmarchicus*

The relationship between temperature (at 50 m depth) and daily egg production was insignificant (linear regression, $R^2$=0.042, p=0.503) (Figure 10).

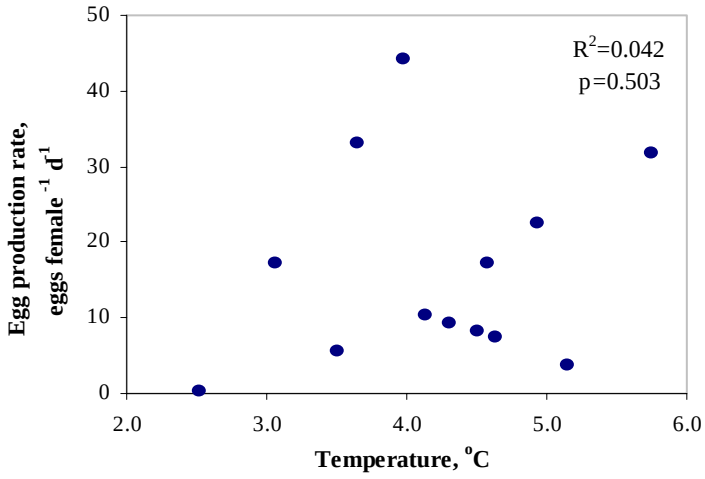



**Figure 10: Relationship between temperatures at 50 m and egg production rates of *Calanus finmarchicus*. The coefficient of determination and the significance level of a linear regression model are shown on the graph.**

The linear regression between concentration of chlorophyll *a* and egg production rate was significant (Figure 11), but the relationship wasn't very strong ($R^2$=0.376, p=0.026). If the point with the highest concentration of chlorophyll *a* is excluded from the regression the relationship becomes insignificant ($R^2$=0.004, p=0.841).

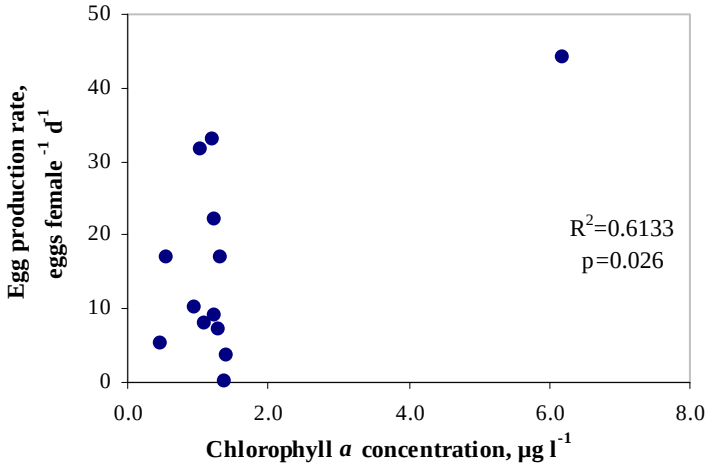



**Figure 11: Relationship between concentrations of chlorophyll *a* and egg production rates of *Calanuc finmarchicus* females. The coefficient of determination and the significance level of a linear regression model are shown on the graph.**

The relationship (linear regression model) between gut content of the females and their egg production rate was significant ($R^2$=0.463, p=0.029) (Figure 12). However, if the point with the highest gut content of the females is excluded the relationship becomes insignificant ($R^2$=0.025, p=0.662).

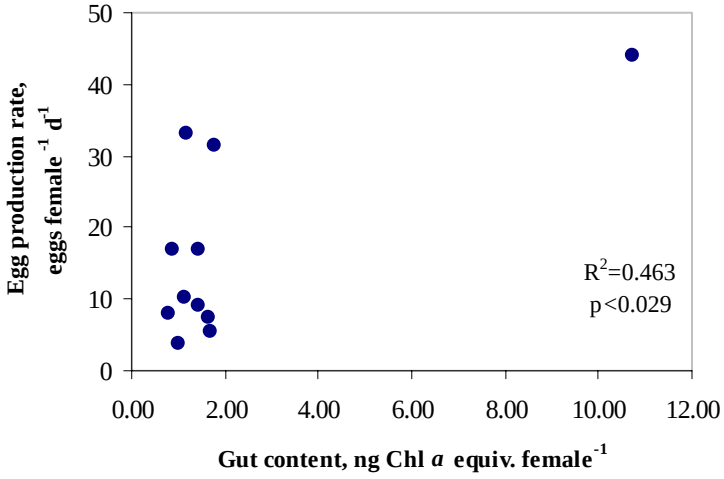



**Figure 12: Relationship between the gut content and egg production rate of *Calanus funmarchicus* female. The coefficient of determination and the significance level of a linear regression model are shown on the graph.**

A linear regression between presume length of *Calanus* females and its egg production rate was not significant ($R^2$=0.011, p=0.27) (Figure 13).

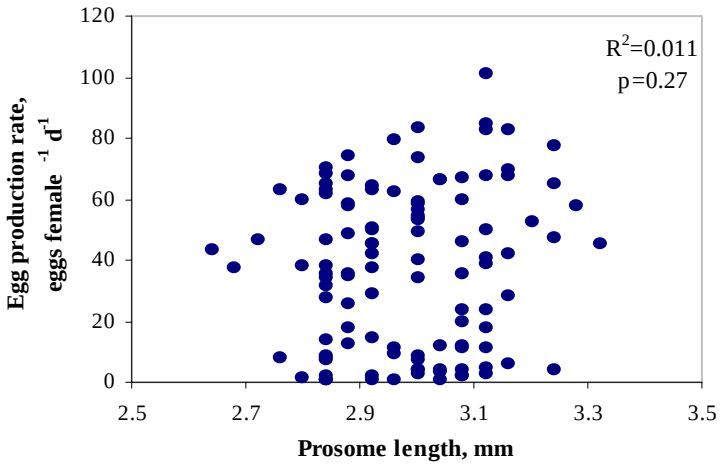



**Figure 13: Relationship between presume lengths and egg production rates of *Calanus finmarchicus*. The coefficient of determination and the significance level of a linear regression model are shown on the graph.**

Linear regression between weight of *Calanus* females and egg production rate was insignificant ($R^2$=0.000, p=0.922) (Figure 14).

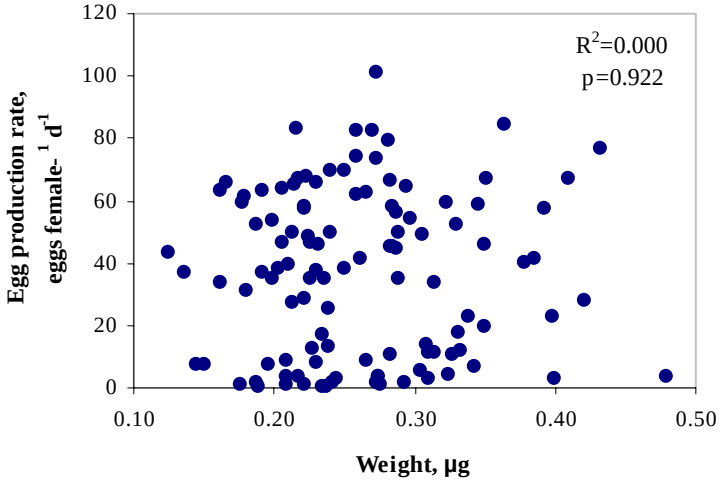



**Figure 14: Relationship between weights and egg production rates of *Calanus funmarchicus*. The coefficient of determination and the significance level of a linear regression model are shown on the graph.**

## 4.9 Comparison between water masses

There was not significant difference (t-test, p=0.229) in the concentration of chlorophyll *a* in Arctic (1.5 µg $l^{-1}$) and Atlantic (1.2 µg $l^{-1}$) water (Figure 15). However, chlorophyll *a* concentration varied greatly within the Arctic water (0.3-6.2 µg $l^{-1}$).

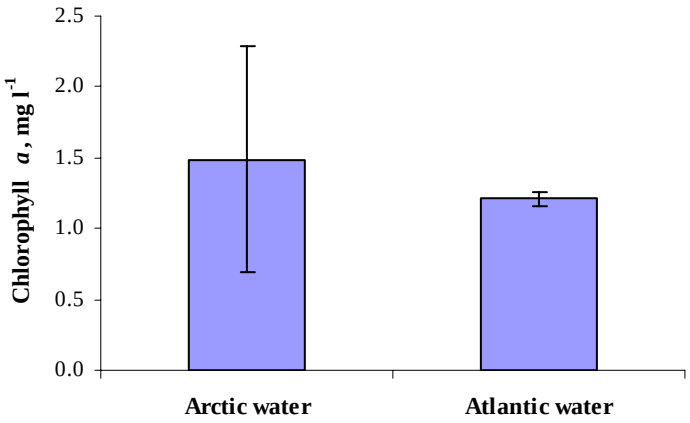



**Figure 15: Mean chlorophyll *a* concentrations in the Arctic and Atlantic water. Vertical lines show standard error.**

The average abundance of zooplankter was higher in the Atlantic water (~73 000 and. $m^{-2}$) than in the Arctic water (~50 000 and. $m^{-2}$) (Figure 16). The difference was almost significant (t-test, p=0.078).

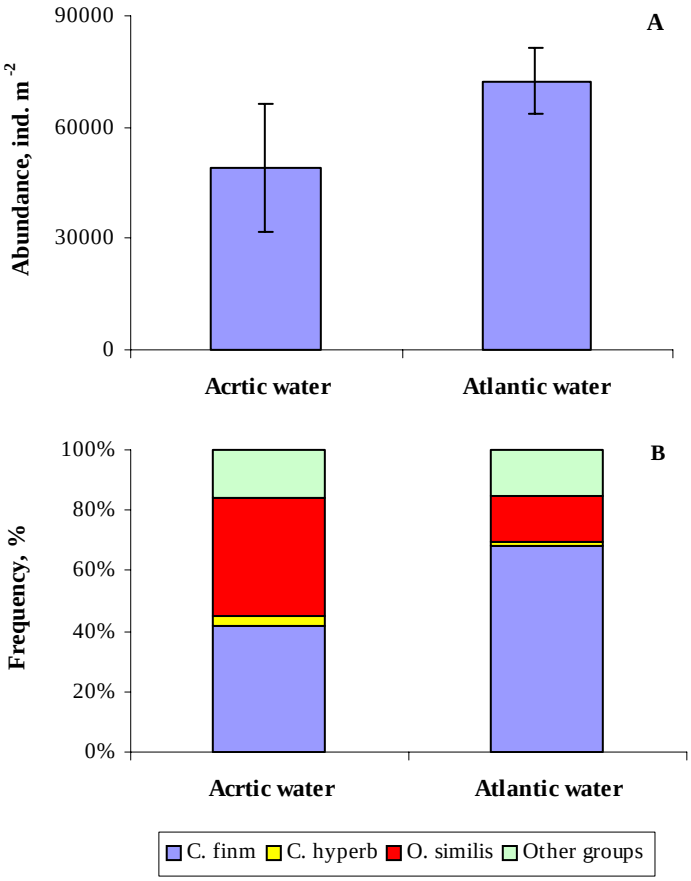



**Figure 16: Number of total zooplankton (and. $m^{-2}$) (A) and relative frequency of most numerous zooplankton taxa (B) in the Arctic and Atlantic water. Vertical lines show standard error.**

The abundance of *Calanus finnarchicus* was more than two times higher in the Atlantic water (~50 000 ind. $m^{-2}$) than in the Arctic water (~22 000 ind. $m^{-2}$) (Figure

17). The difference was almost insignificant (t-test, p=0.086). Age structure in the Arctic and the Atlantic water was almost the same, but nauplii and males were observed only in the Atlantic water.

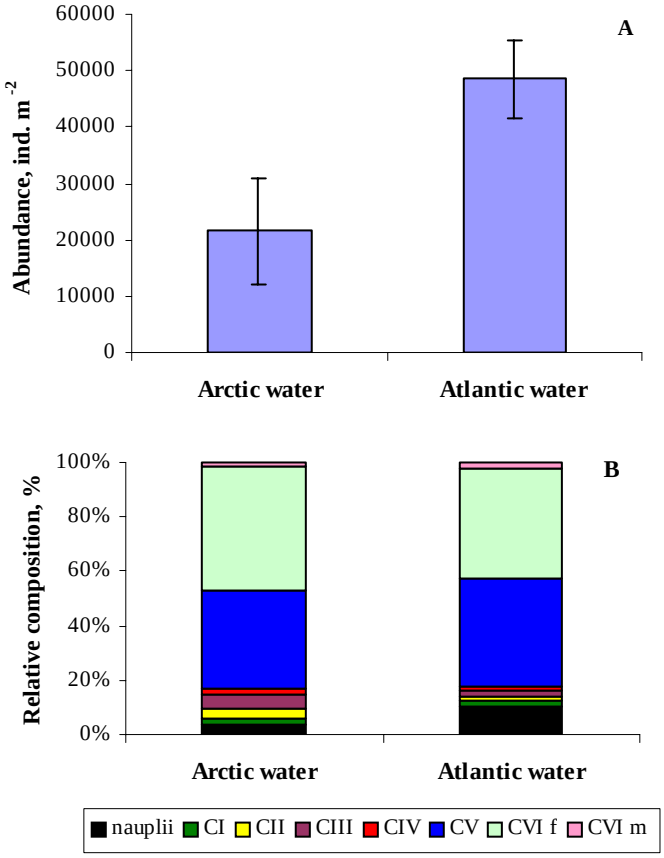



**Figure 17: Number of *Calanus finmarchicus* (ind. m$^{-2}$) (A) and relative number of copepod stages (B) of by stage in the Arctic and Atlantic water. Vertical lines show standard error.**

Gut content of *C.finmarchicus* female was significantly higher (t-test, p<0.01) in the Arctic water (~6 Chl *an* equiv. ng female$^{-1}$) than in the Atlantic water (~1.3 Chl *an* equiv. ng female$^{-1}$) (Fig. 18). But the considerable difference in gut content of the females within the Arctic water was observed (1.4-10.7 Chl *an* equiv. ng female$^{-1}$).

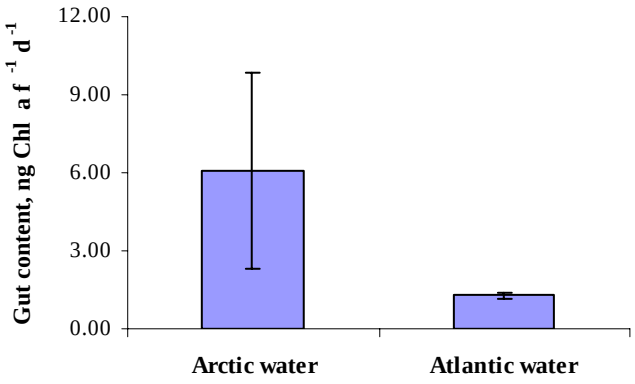



**Figure 18: Mean gut content of female *Calanus finmarchicus* in the Arctic and Atlantic water. Vertical lines show standard error.**

The proportion of the mature females was higher (72%) in the Atlantic water compared to the Arctic water, whereas in the Arctic water the proportion of the immature females (gonad stages 1-3 combined; 31%) was higher than in the Atlantic water (gonad stages 1-3 combined; 20%) (Figure 19). Females with spent gonads were only observed in the Atlantic water.

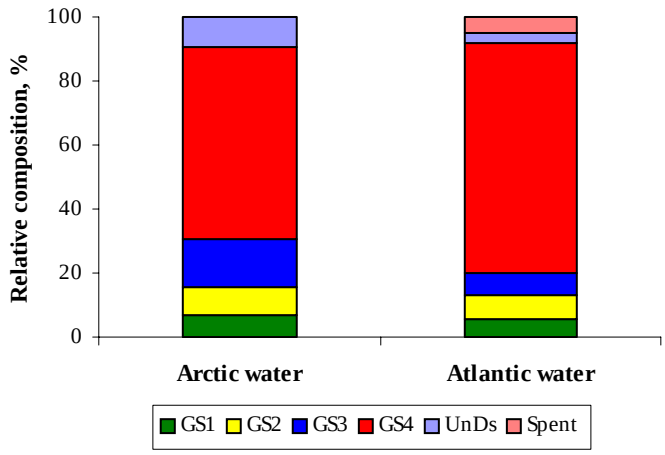



**Figure 19: Relative frequency (%) of gonad stages of *Calanus finmarchicus* females in the Arctic and Atlantic water.**

Higher egg production rates was observed in the Arctic water (on average 20 eggs female$^{-1}$ d$^{-1}$) than in the Atlantic (on average 15 eggs female$^{-1}$ d$^{-1}$) (Figure 20), but the difference was not significant (t-test, p=0.224). The maximum egg production (44 eggs female$^{-1}$ d$^{-1}$) was recorded within the Arctic water. However, daily egg production varied greatly especially in the Arctic water (between 0 and 44 eggs female$^{-1}$ d$^{-1}$).

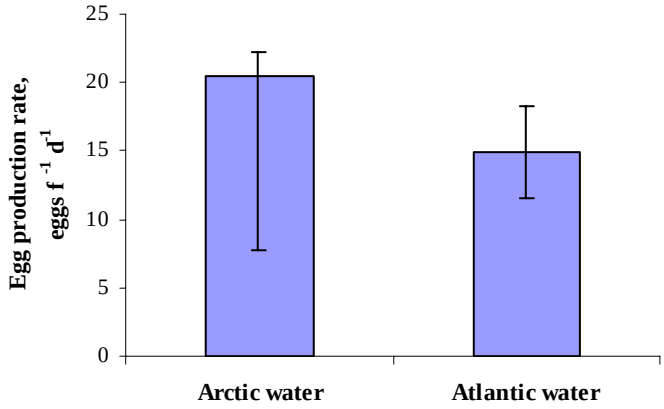



**Figure 20: Mean egg production rates of *Calanus finmarchicus* (eggs female$^{-1}$ d$^{-1}$) in the Arctic and Atlantic water. Vertical lines show standard error.**

# 5 DISCUSSION

The western Norwegian Sea is affected by the warm and cold currents, the cold East Icelandic Current coming from the northwest and warm Atlantic Currents from the southeast, southwest and the northeast (Figure1). According to the results the investigation area is influenced mainly by warm Atlantic water (T~3-8°C and S>34.9 psu, Malmberg and Valdimarsson 2003) as mean temperature was 3.8°C and mean salinity was 34.9 psu (Figure 3). However, in the northwest the influence of Arctic Water (T<0-2°C, S=34.3-34.9, Malmberg and Valdimarsson 2003) is pronounced.

Higher chlorophyll *a* concentrations were observed in the western part of the study area, suggesting an east-west gradient in phytoplankton development. This is confirmed by data on nutrients concentration (K. Guðmundsson, pers. comm.). In the east the nutrient concentrations were relatively high (K. Guðmundsson, pers. comm.) and therefore it is likely that the bloom had not reached its peak at the time of study. On the other hand, in the southwest (Stns 345, 350, 352) the nutrients were almost exhausted so the bloom had most likely finished there (K. Guðmundsson, pers. comm.).

The present study shows that copepods are dominant in the western Norwegian Sea in May. The results further show that *C. finmarchicus* is the most abundant species (Figure 6). This is in accordance with other studies in the Norwegian Sea (Wiborg 1955, Timochina 1969, Assthorsson *et al.* 1983, Gislason and Astthorsson 2002). The portion of the larger Arctic species such as *C. hyperboreus* and *Metridia longa* was relatively high in water influenced by the cold East Icelandic Current, where replacement of boreal faunas by arctic species was observed (Figures 5 and 16). However, due to their larger sizes both species are more important in terms of biomass than numbers.

*C. finmarchicus* population was comprised mostly of individuals in copepod stage CV and females (Figure 8). Considerable difference in *Calanus* abundance between the stations was observed, whereas the age structure was nearly the same. In the southeast, eggs and nauplii of *C. finmarchicus* were observed and it may indicate reproductive activity there. Spent females were found on two stations in the northeast. Thus it seems that the spawning activity of *Calanus* had ceased there. According to Niehoff *et al.* (1999) mainly females of *C. finmarchicus* dominated at the Weather Station M at the end of May, but their abundance was much lower (~2 000 ind. $m^{-2}$) than we have found (~17 000 ind. $m^{-2}$, Figure 6). Hirche *et al.* (2001) and Gislason and Astthorsson (2002) also observed similar age composition of *C. finmarchicus* in the spring-early summer period. Thus the age structure of the population of *Calanus* shows that the over wintering animals were reproducing and the new spring generation developing.

The average gut content of *C. finmarchicus* ranged between 0.8 and 10.7 ng Chl *a* equiv. $female^{-1}$) (Figure 7). In the Barents Sea Tande and Båmstedt (1985) found that the gut content of adult females of *C. finmarchicus* varied between 2-24 ng $copepod^{-1}$ during the spring blooming. Simard *et al*. (1985) reported that the value of gut content was 1-4 ng $copepod^{-1}$. This was also observed by Boyd and Smith (1980). The present result shows that ambient phytoplankton concentration is related to the value of gut content (Figurs 4 and 7).

The pressure of eggs and nauplia shows that *C. finmarchicus* had started to reproduce before the sampling. The sex ratio (females: males) varied between 6: 1 and 72: 1. Low abundance of males indicates spawning activity. The proportion of mature *C. finmarchicus* females was high (69% on average). The lowest proportion of mature females was observed in the northwest (Figure 9), in waters of cold East Icelandic Current. Changes in age structure of *Calanus* population toward an increasing number of nauplia and early copepodites, low number of males and presence of spent females at some stations (Stns 332, 334, 340, 343) and high egg production rates (Stn 350) indicated active processes of reproduction and development of the new generation in the area.

The data showed that mean egg production of *Calanus* was 16 eggs female$^{-1}$ d$^{-1}$ (range for all the stations 0-102 eggs female$^{-1}$ d$^{-1}$). Runge (1985) observed daily egg production of *C. finmarchicus* of 13-29 eggs female$^{-1}$ d$^{-1}$ in the sea off Nova Scotia. In the Greenland and Norwegian seas *Calanus* lays 12-14 eggs female$^{-1}$ d$^{-1}$ according to results by Hirche (1990). In the Gulf of St. Lawrence Ohman and Runge (1994) reported egg production rates in the range 11-45 eggs female$^{-1}$ d$^{-1}$. In fjords in northern Norway *C. finmarchicus* produce on average 22 eggs female$^{-1}$ d$^{-1}$ in April (Diel and Tande 1992) and in the open Norwegian Sea it produced 65 eggs female$^{-1}$ d$^{-1}$ (Harris *et al*. 2000). Niehoff *et al*. (1999) presented data from the Weather Station M that egg production rate was 12 eggs female$^{-1}$ d$^{-1}$ in the pre-bloom period and 35 eggs female$^{-1}$ d$^{-1}$ during phytoplankton bloom when 100% of mature females observed.

Since no significant relationship was found between egg production rates of *Calanus* females and ambient temperature (Figure 10) it seems that other factors may influencing reproduction of *Calanus*. At experimental conditions egg production rate increased with increasing temperatures (Hirche *et al.* 1997, Campbell and Head 2000a). Nevertheless, Hirche (1990) reported that *C. finmarchicus* females may produce eggs even at low temperature. Harris *et al.* (2000) concluded that temperature plays a small role in egg production rates for the two *Calanus* species. In the western Norwegian Sea the relationship between egg production rate of *C. finmarchicus* and concentration of chlorophyll *a* and gut content of females is questionable as well. Previous studies (Hirche *et al.* 1997, Niehoff *et al.* 1999, Campbell and Head 2000a) show that egg production of *Calanus* increased with increased of food concentration and Niehoff (2000) showed that reproduction is under food-supply control. However, Harris *et al*. (2000) observed that the maximum egg production of *C. finmarchicus* and *C. helgolandicus* females were at lower concentration of chlorophyll *a*. The results showed no significant relationship between presume length of *C. finmarchicus* females and its egg production rate (Figure 13). The relationship between female's weight and its egg production rate was also insignificant (Figure 14). Similar results on two species of *Acartia* presented by Jónasdóttir (1994). Hirche (1990) also found insignificant correlation between female's body length and its clutch size. However, Niehoff *et al*. (1999) suggested that bigger females could be the reason of higher egg production rates. Runge (1985) and Runge and Plourde (1996) found a significant increase in clutch size with female body size at experimental conditions. The considerable difference in hydrograph, an east-west gradient in the spring phytoplankton development and the pressure of females at different state of gonad development may in combination affect reproduction of *C. finmarchicus*.

Some differences between Arctic and Atlantic waters were observed. Thus, gut content and egg production rate of *C. finmarchicus* females were higher in Arctic water (Figures 16 and 20), whereas zooplankton abundance was higher in Atlantic water (Figures 17 and 18). Higher proportion of mature females, pressure of spent females, and nauplia in Atlantic water may indicate more active reproduction activity in *C. finmarchicus* population there.

## 6 CONCLUSIONS

- The western Norwegian Sea is influenced by cold Arctic water warm Atlantic water.
- An east-west gradient in the spring phytoplankton development was observed.
- *Calanus finmarchicus* dominated the zooplankton community in the western part of the Norwegian Sea (42-92% of all zooplankton in terms of numbers).
- Data on age composition of *C. finmarchicus*, state of females maturation and egg production indicated that the population was reproducing.
- Feeding activity of *C. finmarchicus* was rather low and may reflect low food supply.
- No statistically significant relationship was found between egg production of *C. finmarchicus* and temperature, chlorophyll *a* concentration, female gut content, presume length and weight.
- In cold Arctic water feeding and reproduction activity of *C. finmarchicus* population was higher than in the Atlantic water. In contrast zooplankton abundance was higher in warmer Atlantic water than in the cold Arctic water.

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