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Published in:
Deep-Sea Research Part I: Oceanographic Research Papers

Link to article, DOI:
10.1016/j.dsr.2021.103508

Publication date:
2021

Document Version
Peer reviewed version

Citation (APA):
Kristiansen, I., Jónasdóttir, S. H., Gaard, E., Eliasen, S. K., & Hátún, H. (2021). Seasonal variations in population dynamics of Calanus finmarchicus in relation to environmental conditions in the southwestern Norwegian Sea. *Deep-Sea Research Part I: Oceanographic Research Papers*, *171*, Article 103508. https://doi.org/10.1016/j.dsr.2021.103508

Journal Pre-proof

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PII: S0967-0637(21)00047-9

DOI: https://doi.org/10.1016/j.dsr.2021.103508

Reference: DSRI 103508

To appear in: *Deep-Sea Research Part I*

Received Date: 12 August 2020

Revised Date: 7 January 2021

Accepted Date: 6 March 2021

Please cite this article as: Kristiansen, I., Jónasdóttir, Sigrú.H., Gaard, E., Eliasen, Sóá.K., Hátún, Hjá., Seasonal variations in population dynamics of *Calanus finmarchicus* in relation to environmental conditions in the southwestern Norwegian Sea, *Deep-Sea Research Part I* (2021), doi: https://doi.org/10.1016/j.dsr.2021.103508.

Seasonal variations in population dynamics of *Calanus finmarchicus* in relation to environmental conditions in the southwestern Norwegian Sea

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Keywords: Atlantic Water; East Icelandic Water; vertical distribution; reproduction; lipid content; diapause

Abstract

A seasonal study of the life cycle and reproductive biology of the copepod *Calanus finmarchicus* – the dominant zooplankton species and a key link between the lower and higher trophic levels within the southwestern Norwegian Sea - is presented. *C. finmarchicus* reproduces, feeds and accumulates lipids during spring and summer within surface waters, which enables it to survive overwintering at depth until the following spring. An inflow of warm and saline Atlantic Water (AW) enters from the southwest and meets the cold and less saline subarctic waters (SAW) flowing from the north and west. This confluence establishes the dynamic Iceland Faroe Front. The study includes seven cruises, conducted from July 2013 to July 2014. Ascent occurred earlier and over a prolonged period in AW compared to the SAW. The peak egg production per capita occurred in April (43 eggs female^{-1} d^{-1}) and May (13 eggs female^{-1} d^{-1}) in SAW and AW, respectively. The higher productivity in SAW can be explained by larger female size, increased lipid content and better feeding conditions. The increased egg production rates in May in AW were not reflected in an increased abundance of young copepodite stages in June, potentially due to a decoupling between early ascent and the late onset of the bloom. Descent, largely comprised by the pre-adult stages, to overwintering depths was already initiated in June in both regions. This coincides with increased lipid content, being significantly higher at depth compared to the surface in late summer. A smaller portion of individuals remained within the upper layers to spawn a second

generation in August in both regions, increasing the abundance and biomass. The reproductive phenology and stage development of *C. finmarchicus* likely influence feeding and competition between herring and mackerel and the duration of their stay in Faroese waters.

1.0 Introduction

The copepod *Calanus finmarchicus* is the dominant secondary producer within the Norwegian Sea (Wiborg, 1955; Melle et al., 2014). It is an intense grazer of phytoplankton and serves as an important food source for the large stocks of pelagic fish such as Norwegian spring spawning herring and mackerel that migrate to this area to feed during spring and summer (e.g Dalpadado et al., 2000; Gislason and Astthorsson, 2002; Debes et al., 2012).

The success of *C. finmarchicus* is partly due to its ability to survive long periods during low food supply and to reduce predation mortality in winter (Jónasdóttir et al., 2019). The pre-adult copepodites have adopted an overwintering strategy where they migrate to great depths and enter a resting state (diapause) (Ingvardsdóttir et al., 1999). During this period, the animals live off their accumulated lipid reserve, particularly of the wax esters, which comprise the highest proportion of the total lipid content (Falk-Petersen et al., 2009). The duration of diapause is likely influenced by the amount of lipid content, overwintering temperatures and geographic location (Jónasdóttir et al., 2019). Towards spring, when favourable feeding conditions return, the copepods ascend back towards the surface where they moult into adults and initiate reproduction (Melle et al., 2004). The energy required for reproduction mainly comes from ingested food. However, the lipid reserve is also assumed to be an important energy source immediately after ascendance to the surface (Heath and Jónasdóttir, 1999; Saumweber and Durbin, 2006). Females spawn either before or during the spring bloom. The eggs are released into the near surface layers, where they hatch and develop through six naupliar and five copepodite stages. Some individuals may moult into the adult stage and start a second round of reproduction while others descend and enter diapause at stage C5 (Melle et al., 2014).

The overwintering depth for *C. finmarchicus* varies geographically (Heath et al., 2000a; Melle et al., 2004). In the Norwegian Sea, the overwintering population is concentrated between 600 to 1200 m depths, which is within in Norwegian Sea Deep Water and Norwegian Sea Arctic Intermediate Water – hereafter collectively referred to as simply Deep Water (Heath et al., 2000b; Edvardsen et al., 2006). The Norwegian Basin, which is located in the southern part of the Norwegian Sea, is a major overwintering area (Heath et al., 2000a; Melle et al., 2004). The presence of a cyclonic gyre within the Norwegian Basin (Jakobsen et al., 2003), aggregates and helps to retain the overwintering population (Melle et al., 2014). Individuals who are not residing within the cyclonic boundary current, are likely transported southwards by the deep water current, through the Faroe-Shetland Channel (FSC) and out into the Iceland and Rockall basins (Gaard and Hansen, 2000; Heath et al., 2000a; Chafik et al., 2020).

C. finmarchicus is also found in high concentrations within the Iceland Sea (Astthorsson and Gislason, 2003; Gislason and Silva, 2012). This cooler environment sustains *C. finmarchicus* with a one year life cycle (Astthorsson and Gislason, 2003) and overwintering depths between 200 to 600 m, which is somewhat shallower compared to Norwegian Basin (Gislason, 2018). From the north-eastern region of Iceland, the copepod is advected into the southwestern Norwegian Sea (Wiborg, 1955; Kristiansen et al., 2019).

Due to the inflow of subarctic waters from the Iceland Sea, the southwestern Norwegian Sea has a more Arctic character than the central and some parts of the northern areas within the Norwegian Sea (Blindheim, 2004). The area is characterized by the persistent and dynamic Iceland-Faroe Front (IFF), which is established when the poleward flow of warm and saline Modified North Atlantic Water, hereafter abbreviated to Atlantic Water (AW) (Hansen and Østerhus, 2000), meets the southeastern flow of cold and fresh East Icelandic Water from the Iceland Sea (Fig. 1a). The posture of the IFF slopes downwards from the surface in the north toward the Iceland-Faroe Ridge/northern Faroe Plateau further south (Fig. 1) (Hansen and Østerhus, 2000). The AW flows eastwards along the southern border of the IFF, converges into the Faroe Current and progresses further northeastwards along the Norwegian slope. A fraction of the poleward flow re-circulates back towards the Faroe Islands along the Jan Mayen Ridge as the Recirculated Faroe Current, carrying Norwegian North Atlantic Water. The water masses within the subarctic region, north of the IFF, are hereafter collectively termed Subarctic Waters (SAW).

A standard monitoring section, named Section N, extends northwards from the Faroe Islands and into the southwestern Norwegian Sea (Fig. 1a). In the near-surface layer, the transect covers AW in the southern region and SAW in the northern region, and these are separated by the IFF (Fig. 1b). Deep Water occupies the water column below approximately 500 m.

A key factor that determines the spatial distribution of *C. finmarchicus* is its position in the water column as this determines its advection route (Heath et al., 2000a). The most direct transportation route of *C. finmarchicus* to the southern region of Section N is with the AW from the northeastern Iceland Basin. There, a low standing stock of overwintering individuals (Heath et al., 2004) and low reproduction activity within the upper layers in spring (Jónasdóttir et al., 2008) have been documented. It has also been suggested that *C. finmarchicus* may derive from the deep overflow from the Norwegian Sea and the FSC via the Faroe Bank Channel (FBC) west of the Faroe Islands (Heath and Jónasdóttir, 1999; Gaard and Hansen, 2000; Jacobsen et al., 2017). During ascent, a portion may enter the warm upper layers of AW and circulate within the offshore waters around the Faroe Islands (Gaard and Hansen, 2000; Heath 1999).

The origin of the water masses north of the IFF suggest that the *C. finmarchicus* individuals within the subarctic region of Section N are a mixture of the populations from the Norwegian and Iceland Seas (Wiborg, 1955; Bucklin et al., 2000; Kristiansen et al., 2019). Furthermore, Kristiansen et al. (2019) found a positive correlation between *C. hyperboreus*, an expatriate

from the Iceland Sea, and the volume of subarctic waters from the Iceland Sea, i.e. when increased transport of subarctic waters from the Iceland Sea crosses the subarctic region along Section N, the abundance of *C. hyperboreus* increases. The signal was less clear for *C. finmarchicus* as it successfully overwinters and reproduces both in the Iceland and Norwegian Seas. However, since 2003, a phenological change in the *C. finmarchicus* population in SAW (Kristiansen et al., 2016) has co-occurred with a reduction of subarctic waters from the northwest and *C. hyperboreus* (Kristiansen et al., 2019). Before 2003, initiation of reproduction along Section N occurred earlier in AW compared to SAW, resulting in different life cycles and stage compositions in the two water masses (Gaard, 1996; Kristiansen et al., 2016). The phenological shift in 2003 resulted in similar reproductive pattern along Section N. Before 2003 only one generation of *C. finmarchicus* was produced north of the IFF whereas after this, the production of two generations is evident (Gaard, 1999; Kristiansen et al., 2016). To further investigate the demography of *C. finmarchicus* at Section N, a seasonal study was conducted, which is the focus of the present study.

Here, seasonal abundance and stage composition of *C. finmarchicus*, combined with vertical distribution, egg production, feeding activity and lipid content north and south of the IFF, are investigated. This is the first time a study has been conducted within the southwestern Norwegian Sea that deals with seasonal vertical investigations. The lipid content, coupled with vertical distribution, throughout the season presents a unique time series. Emphasis is also on comparing the biological characteristics to environmental variables including hydrography and phytoplankton biomass. Possible implications for the feeding conditions for the large pelagic fish stocks within the study area are tentatively discussed.

2.0 Materials & Methods

2.1 Location and sampling

Section N is comprised of 14 stations located from 62°20’N to 64°30’N at longitude 6°05’W, apart for station N14, which is located at longitude 6°00’W (Fig. 1a). The distance between stations is 10 nautical miles. To measure *C. finmarchicus* vital rates, the present study used two sampling stations, N4 and N5, to represent the warmer Atlantic region (AW) and two stations, N13 and N14, to represent the colder subarctic region (SAW) (Fig. 1b). Samples were collected on seven occasions over a one-year cycle (Table 1). During every sampling occasion, hydrographic data (temperature and salinity), chl-*a* fluorescence and zooplankton samples were collected in order to examine the seasonal dynamics and demography of *C. finmarchicus* and its habitat.

2.2 Hydrography

A CTD (Seabird Electronics 911 Plus) was used to measure the profiles of temperature and salinity to 1000 m depth. In July 2013 and 2014, a smaller CTD (Seabird 25) was used which

was lowered down to 500 m. Salinity was calibrated against standard seawater with an Autosal 8400A salinometer. A fluorometer was attached to the CTD, measuring the fluorescence profile simultaneously with the hydrographic properties. Raw fluorescence values were used to represent the relative phytoplankton biomass.

2.3 Satellite data

Eight-days temporal averages of level 3, merged (MODIS, VIIRS in varying constellations), GSM-gridded (Maritorena et al., 2002) chlorophyll (CHL1) with 4-km grid resolution, for an area covering Section N (6.5° - 5.5° W by 62.3° - 65° N) for the period 2013 to 2014 from the GlobColour Project, distributed by ACRI-ST, were downloaded from http://www.globcolour.info. The surface chlorophyll variation is presented with a Hovmüller diagram, where the values were spatially smoothed by averaging longitudinally across Section N (6.5° - 5.5° W, i.e. 46-49 km), and laterally by dividing the region into ten 23 km wide segments. By demanding only one valid measurement in each cell in order to compute the chlorophyll level, a relatively good coverage is obtained for the area.

2.4 Seasonal dynamics and demography of *C. finmarchicus*

2.4.1 Seasonal vertical distribution, abundance and biomass

Zooplankton samples were collected with a Multinet (0.25 m^2 opening and 5 nets attached with a 200 µm mesh size) which was hauled vertically from a maximum depth of 1000 m to the surface. The towing speed was 0.3-0.5 m s^{-1}. The upper 200 m had sampling intervals of 50 m. At greater depths, the sampling intervals were adjusted according to the bottom depth or maximum sampling depth. Zooplankton samples were preserved in 4 % formaldehyde solution. In the laboratory, samples were split into subsamples to contain around 200 to 300 individuals of *C. finmarchicus* that were grouped into developmental stages and counted. The prosome length of the first 10 individuals for each stage was also measured to the nearest two decimal places. The number of stages per sample was converted to a mean concentration per m^3 or per m^2 when looking at total water column abundance. The abundance of each developmental stage was converted to biomass based on the allometric relationship between individual body mass and average prosome length proposed by Hay et al. (1991). The formulas $DW=0.0154 *L^{2.71}$ and $DW=0.0073 *L^{3.46}$ were used for stage C1-C5 and adults, respectively, with DW being individual dry weight (mg) and L is prosome length (mm).

2.4.2 Egg production

Females for egg production were collected using a WP-2 net with a 200 µm mesh size and a 2 L non-filtering cod-end. The WP-2 net was hauled from 50 m depth to the surface with a speed of 0.3-0.5 m s^{-1}. Whenever possible, 20 active and apparently undamaged females were collected and individually transferred into 0.5 L incubation chambers, with a fitted 500 µm mesh screen on the bottom to separate the female from the eggs produced. The chambers were filled up with 20 µm filtered seawater taken from 3 m depth. The females were

incubated for approximately 24 hours in dim light at *in situ* temperatures. Following the incubation period, the content of the chamber was filtered through a 30 µm sieve and the eggs counted under a stereomicroscope. The proportion of females that spawned during the incubation period is referred to as "spawning frequency", which is expressed as percentage per day. Females that produced > 1 egg are included. Based on this data, individual (eggs female^{-1} day^{-1}) and community (eggs m^{-2} day^{-1}) egg productions rates (EPR) are calculated. If less than 5 females were found, the sample is not representative due to large variations and thus excluded from the experiment.

2.4.3 Female gut content

Samples were collected with a WP-2 net which had a cod-end fitted with a 200 µm net screen. The WP-2 net was towed vertically from 50 m depth towards the surface. A sufficient portion of zooplankton was quickly transferred to zip-bag and immediately sprayed with freezing spray to prevent the animals to defecate. Subsequently the sample was placed in the freezer at -20°C. To prevent sample deterioration, samples were analysed within three months. The working procedure for measuring and calculating the gut fluorescence was done according to Blåmstedt et al. (2000). Whilst keeping the sample cold, five females were quickly selected and transferred into a vial and where the gut pigments (i.e. chl *a*) were extracted with acetone and measured with a Turner Model 10 fluorometer. To minimize high variability, six replicates were made per sample.

2.4.4 Lipid analysis

Animals for lipid analysis were taken from the same net hauls as the samples used for gut fluorescence analysis. The zooplankton was handled delicately, put into vials and subsequently frozen in liquid nitrogen. After the cruise, the samples were transferred to a freezer, which kept them preserved at - 84°C. Prior to analysis, the samples were sorted while kept on ice. The prosome length of two or three intact copepods of stage C5 and females was measured and subsequently placed in tapered 1.5 ml vials. Three replicates were made. The lipids were extracted according to the Folch method (Folch and Sloane-Stanley, 1957). Chloroform:methanol (2:1), a known concentration of the internal standard, Ketone, and a 0.88% KCL solution were added to each vial as the initial step in the lipid extraction process. The air in the vials was replaced by nitrogen gas and subsequently stored at -84°C. The samples were shipped on dry ice to DTU Aqua (Denmark) for further analysis, using an Iatroscan TLC (thin layer chromatography) as described in Jónasdóttir (1999). The main lipid reserve, i.e. the wax esters, were analysed and quantified in this paper.

2.5 Data analysis

All data was checked for normality and transformed if necessary. Comparison of means between AW and SAW was conducted using the independent two-sample t-test or the equivalent non-parametric Mann-Whitney *U* test. A Principal Component Analysis (PCA) was used to detect causality between EPR and the environmental variables within the study

area during the peak egg production period from April to May. Data and statistical analyses were performed using R core Team.

3.0 Results

3.1 Hydrography and fluorescence

Temperature and salinity profiles south and north of the IFF were clearly different (Fig. 2). Within the upper 50 m, the seasonal temperature steadily increased from February to August measuring between 7.5 to 11.2 °C in AW (Fig. 2a) and 3.4 to 8.9 °C in SAW (Fig. 2d). The salinity fluctuated along with the temperature variability (Fig. 2b and 2e).

Snapshots of the chl-*a* fluorescence was captured during the CTD measurements at each cruise (Fig. 2c and 2f) and is supported by satellite measurements of the seasonal progression of the phytoplankton biomass which provides an overview of the conditions before, during and after the sampling dates (Fig. 3). According to Eliasen et al. (2017) satellite observations capture on average lower values compared to spectrophotometric analysis of water samples by around a factor of 2. However, keeping this in mind, the usage of satellite data provides high frequency (and spatially extensive) observations, which is valuable alongside less frequent ship collected data. The primary production started earlier in SAW compared to AW. In 2013, the onset of phytoplankton production north of the IFF started around mid May, while south of the IFF the bloom started in late May (Fig. 3a and 3c). From June to August, the bloom was notably higher in the southern region than in the northern region. In 2014, a similar pattern can be observed as in 2013, apart from the four week earlier initiation of spring production north of the IFF (Fig. 3b and 3d).

3.2 Seasonal vertical distribution

In February, 98% of the collected overwintering population (G_0) in SAW, which mainly comprised of the pre-adult stage C5, was found between 500 m to 1000 m in depth (Fig. 4j). In contrast, 44% of the collected G_0 population in AW was found within the upper 200 m (Fig. 4c), suggesting that the ascent to the surface layers is more advanced in AW. It is, however, possible that a lesser amount of overwintering individuals were located below the maximum sampling depth of 1000 m. In April, 95% and 65% of the total G_0 population resided within the upper 50 m in SAW and AW, respectively. The remaining G_0 individuals in AW were located between 50-500 m in depth. Within the upper 50 m, the adult stages dominated the population, comprising 50% and 70% of the population in SAW and AW, respectively. Initiation of reproduction in April was evident, particular in SAW, where the abundance of stage C1 was higher compared to south of the IFF (Fig. 4d and 4k). In May, the recruits (stage C1 to C3) clearly dominated the population structure (Fig. 4e and 4l), while in June the juveniles (stage C4 and C5) also constituted a large portion of the *C. finmarchicus* population (Fig. 4f and 4m). In July, the total abundance within the upper 50 m had only

declined by 9% in AW, while the *C. finmarchicus* stock in the SAW declined by 78% compared to June (Fig. 4g and 4n).

Evidence of descent to diapause appeared already in June, where throughout the water column, around 2% of the juveniles and adults appeared at > 200m depth north and south of the IFF, respectively. By July, these numbers had increased to 18% and 14% in AW and SAW, respectively and resembling the overwintering concentration found north of the IFF in February. Descent of the animals was also apparent in July 2013, also with higher concentration in the south compared to the north (Fig. 4ab and 4h). In August, the overwintering concentration had increased in the subarctic region to a similar level to the warmer region, south of the IFF (Fig. 4b and 4i).

The depth integrated numbers were relative low during winter and early spring (February to April), ranging from around 5,500 individuals m^{-2} in AW and 11,700 individuals m^{-2} in SAW (Fig. 5a and 5c). In May, the numbers in AW increased dramatically to 91,600 individuals m^{-2} due to input of G_1 while a three-fold increase occurred in SAW. In June, a steep increase to 141,376 individuals m^{-2} was observed in SAW. After the steep increase in numbers in May and June, the numbers declined.

Zooming in on stage development within the upper 50 m, which is also the depth layer used for investigating egg production and gut content, we found no significant difference in total abundance throughout the season (Mann Whitney U-test, $p > 0.05$). The composition in the *C. finmarchicus* population in AW (Fig. 6a and 6b) and SAW (Fig. 6e and 6f) bear resemblance early in the season, with an increased number of females in April along with a lower number of stage C1. The number of all developmental stages continues to increase, peaking in May in the AW but a month later in SAW. A subtle difference in the population structure is observed in June and July where AW appears to have a higher proportion of C4 and C5 compared to the population in SAW (Fig. 6b and 6f). Both regions show evidence of an increase in stage C1 in August, which indicates that a secondary production occurs in both regions. The composition in abundance is reflected in the biomass pattern of *C. finmarchicus* within the upper 50 m in AW (Fig. 6c and 6d) and SAW (Fig. 6g and 6h), being lowest in February and highest in May and June in AW (80 mg DW m^{-3}) and SAW (120 mg DW m^{-3}), respectively. There was no significant difference in total abundance and biomass throughout the season within the upper 50 m (Mann Whitney U-tests, $p > 0.05$).

There is a significant difference in female sizes (Welch t-test, $p < 0.05$), with individuals being larger in SAW than in AW within the upper 50 m throughout the season (Fig. 7). The seasonal trend is more pronounced in AW compared to SAW. In February, AW females are at their smallest size while they are largest in April. Hereafter, from May to July, they gradually decrease in size as they have being growing during higher temperature in spring and summer (Durbin et al., 2000). In contrast, the mean size of SAW females remains quite constant from February to July, ranging from 2.53 to 2.58 mm.

3.3 Egg production

The seasonal variability in daily EPR in AW and SAW is shown in Fig. 8, revealing a significant higher production capacity in SAW (Welch t-test, $p < 0.05$). During winter, not enough females were caught to measure the EPR. In April, the egg production had drastically increased in SAW, reaching its peak at 43 eggs female^{-1} d^{-1} (Fig.7e). A notable increase was also observed in AW in April (Fig. 8a), but the peak was recorded in May in this southern region, measuring 13 eggs female^{-1} d^{-1}. In June and July, the egg production remained below 0.2 and 1.3 eggs female^{-1} d^{-1} in SAW and AW, respectively. Similar low values were also noted in July 2013. Based on the concentration of females and individual egg production rates, average community egg production rates were calculated. The community EPR were highest in April, with a subsequent decrease in May in SAW from ~250,000 to ~43,000 eggs m^{-2} d^{-1} (Fig. 8g). In AW, the community EPR increased from 16,000 eggs m^{-2} d^{-1} in April to 91,000 eggs m^{-2} d^{-1} in May (Fig. 8c). The proportion of spawning females from April to July was highest in April and May, ranging between 95 to 97 % in SAW (Fig. 8f) and 85 to 90% in AW (Fig. 8b).

In contrast to the egg production rates, the gut content was significant higher in AW compared to SAW throughout the season (t-test, $p < 0.05$). The gut content was highest in April and May in both regions, which coincides with increased female fecundity. The gut content increased from April to May in AW (Fig. 8d) while in SAW only a slight variation was observed, from 3.0 ng to 3.3 ng Chl *a* female^{-1}, during the same period (Fig. 8h). During summertime, i.e. from June to July, the gut content was significantly lower, remaining below 1.6 ng Chl *a* female^{-1} in both water masses.

Environmental variables and female condition (i.e. size and gut content) influencing the egg production rates in AW and SAW were further examined with a PCA (Fig. 9). In order to extract primary factors influencing the egg production rates during the peak period, data collected from April to May was considered in the analysis. The first and second principal components (PC) explained 48.2% and 29.2%, respectively, of the total variation in the data. Two separate clusters are observed on the basis of PC scores, indicating a clear separation between AW (negative PC1 scores) and SAW (positive PC1 scores). The SAW cluster is positively associated with higher egg production rates, spawning frequency, female size and fluorescence units. In contrast the AW cluster is associated with higher temperatures and gut fluorescence. The PCA reveals that *C. finmarchicus* in SAW have higher egg production rates associated with larger individuals and increased spawning frequency when compared to the warmer AW.

3.4 Lipid content

A seasonal and vertical lipid profile of the C5 pre-adult stage and females in AW and SAW is presented in Fig. 10. There is a general tendency throughout the season that stage C5 has a higher wax ester content compared to the females. Both C5 and females in the northern region tend to have a higher seasonal wax content compared to the individuals found south of the IFF (t-tests, $p < 0.05$), which coincides with larger female size (Fig. 11a). In February, the

lipid concentration for both stages within 0-200 m depth layer was low and became even lower in May but in June and July the levels had increased, particularly for stage C5, indicating that the individuals were preparing for diapause (Fig. 10). The highest wax ester reserves were recorded July at >500 m depth for both stages. While the mean lipid reserve for C5 was up to 40 times higher compared to the females in the upper layer in July in both regions, the wax esters at >500 m depth was similar between the stages, measuring on average 52 and 85 μg^{-1} in AW and SAW, respectively.

4.0 Discussion

Numerous studies on *C. finmarchicus* have been conducted within the eastern, central and northern Norwegian Sea, while few have focused on the southwestern Norwegian Sea. Zooplankton monitoring back to 1994 has shown that prior to 2003, the stage composition of *C. finmarchicus* in May used to be different in the warm AW compared to the colder SAW north of the Faroe Islands (Kristiansen et al., 2016). However, since 2003, a phenological shift occurred, resulting in a similar composition of developmental stages between the areas. Variable volume of the East Icelandic Water relative to the AW affects the ocean climate in the southwestern Norwegian Sea. This variability can be observed between seasons (Hansen and Østerhus, 2000), years (Skagseth and Mork, 2012) and decades (Blindheim et al., 2000). The variability affects plankton composition and phenology and may propel up the food chain to planktivorous predators, including the large herring and mackerel stocks that migrate to the southwestern Norwegian Sea in summertime to feed.

4.1 Horizontal transport

The IFF represents a barrier between the southern and northern regions along Section N (Fig. 2), allowing minimal exchange of copepods across the frontal region (Kristiansen et al., 2016). This vertical barrier results in a clear difference in female sizes between the regions (Fig. 7). The notable difference observed in February could potentially be due to the (i) advection pattern in relation to the position of the individuals in the water column or (ii) females who entered diapause from the year before. The females advected to the AW region of Section N in April and May have likely moulted from stage C5 during winter and early spring within the upper layers. Females in June, July and August are smaller than the individuals in spring as they have been growing during higher temperatures. Throughout the season the females were always larger within the subarctic region and smaller in the warmer region, which agrees with the well established inverse relationship between body size and temperature, e.g. Huntley and Lopez (1992) and Durbin et al. (2000). Similar sizes within colder and warmer regions is also documented throughout a geographically wider region (Jónasdóttir et al., 2019).

The subarctic northern region of Section N is resupplied with the G_0-individuals in spring ascending from the overwintering depths within the Iceland Sea and the Norwegian Basin. During summertime when the individuals remain within the upper layers, transport by surface

currents shapes the *C. finmarchicus* community. The advection route is somewhat more complex south of the IFF due to the current system. The simplest and most direct transportation route is likely with the Faroe Current, which carries AW along the southern border of the IFF (Hansen et al., 2003). The winter abundance of *C. finmarchicus* is somewhat lower south of the IFF compared to the northern subarctic region (Fig. 5). This is in good agreement with the overwintering abundance from the different neighbouring regions from which the population north and south of the IFF are likely advected (Dale et al., 1999; Heath et al., 2000a, 2004; Gislason, 2018).

4.2 Seasonal vertical distribution

4.2.1 Timing and duration of ascent

Although the majority of individuals are found <1000 m, some may also overwinter at greater depth (Heath et al., 2000b; Edvardsen et al., 2006; Gislason, 2018) and these are not represented in this paper. The collected G_0 along Section N were found between 500-1000 m depth in Deep Water during winter. Ascent and moulting into adults at Section N occurs around the same time as reported in the Norwegian Sea (Hirche, 1996; Melle et al., 2004) and FSC (Heath, 1999). Since ~44 % of the collected G_0 population in AW compared to only ~2 % of the G_0 population in SAW was located within the upper 200 m in February suggests an earlier arousal and ascent in AW. The ascent in AW also appears to occur over a prolonged period as G_0 individuals are present at 200-500 m depth in April, which is supported by data from the FSC (Heath, 1999) and FBC (Gaard and Hansen, 2000), east and south of the Faroe Islands, respectively. The few G_0 individuals that remained at depth in March had disappeared in May (Heath, 1999). A less gradual ascent pattern was observed in SAW from February to April. Asynchrony ascendance does not suggest that emergency is triggered by environmental cues (Heath, 1999), which has led to the proposal of a gradual depletion of energy stores (wax esters) as a cue for arousal (Jónasdóttir, 1999; Saumweber and Durbin, 2006; Maps et al., 2012). The lower wax ester content for stage C5 in the southern region than in the northern region in February at 500-1000 m depth (Fig. 10) may be an indication of the difference in depth distribution in north and south of the IFF and why the individuals in AW ascent earlier towards the surface.

4.2.2 Initiation of descent

It is generally stated that *C. finmarchicus* remains active within the upper layers until mid to late summer and then descend to greater depth (Gislason 2018; Melle, 2004). In the Iceland Sea and in the western Norwegian Sea descent occurs somewhere between late August and late November (Gislason, 2018; Strand et al., 2020). In contrast, a reduction in abundance within the surface waters of stage C5 and adults is observed in July in the central/eastern Norwegian Sea (Bagøien et al 2012; Strand et al., 2020). Here, we show evidence of descent in both regions between 200 to 500 m depth as early as in June (Fig. 4f and 4m). In July, the overwintering stages, of which 77% comprised stage C5, were found in increasing numbers at greater depths. A small fraction (3%) of females accompanied the juvenile stages. This is

also observed in the Iceland Sea (Gislason, 2018) and the FSC (Heath and Jónasdóttir, 1999). It is notable that the females in July had accumulated lipids instead of directing their energy towards egg production, thus having equal capacity of wax ester reserves as stage C5. Consequently, these females will be immediately ready to contribute to the reproduction in the following spring, after ascent. The wax ester content was higher at depth in July compared to the surface, suggesting that wax ester fullness may be a trigger for descent.

4.3 Spring and summer production

Fecundity is largely dependent on food availability (Stenevik et al., 2007). Kristiansen et al. (2016) showed that the onset of the phytoplankton bloom along Section N generally occurs around May in the SAW and in early June in the AW (e.g. Fig. 3a), which contrasts the pattern from the rest of the Norwegian Sea (Broms and Melle, 2007; Bagøien et al., 2012). The bloom tends to be shorter and more intense in SAW than in AW due to earlier stratification of a relative shallow, low saline upper layer in SAW (Fig. 2).

It appears that the copepods in SAW also have a physiological advantage from February to April compared to the individuals in AW. The females in the SAW are larger (Fig. 7 and 11a) which is known to be an advantage for increased clutch size (Jónasdóttir et al., 2008; Head et al., 2013) and they tend to have a higher wax ester content (Fig. 11b). The four week earlier initiation of the spring bloom in the northern region (April 2014, Fig. 3b) also provides improved feeding conditions for these copepods. This is reflected both in the individual and the community egg production rates (Fig. 8e) as well as the abundance of young stages within the upper 50 m in SAW in April (Fig. 6e). Supporting these results are observations by Heath et al. (2004) and Jónasdóttir et al. (2008) that showed a strong contrast in lipid content and prosome length between individuals north and south of the Iceland Faroe Ridge, with individuals being in better condition north of the Iceland Faroe Ridge which was also reflected in the egg production rates.

We see low egg production rates in April and May in AW that we cannot explain with the present data, which Gaard and Nattestad (2002) and Jónasdóttir et al. (2008) also observed. Despite the number of females increasing by nearly a two-fold from April to May in AW (Fig. 6a), the EPR only slightly increases (Fig. 8c). The high spawning frequency (> 80%) in AW in April and May (Fig. 8b) suggests that most females had fully mature gonads and thus had the potential to contribute to the population. Although the phytoplankton concentrations were at pre-bloom state in April and mid-May in AW, the female consumption was nearly twice as high south of the IFF compared to north of the IFF (Fig. 8). This is not necessarily surprising since maximum levels of ingestion rates have been observed at relatively low chl *a* levels (Stenevik et al., 2007). Therefore, in this situation, it can be speculated whether food quality suppresses the egg production rates rather than the decoupling between ascent and initiation of the spring bloom.

Peak spawning in AW took place during the pre-bloom phase, reaching a maximum of 13 eggs female^{-1} d^{-1} in May, which is in agreement with other studies, e.g. Niehoff and Hirche

(2000) and Jónasdóttir et al. (2008). When the onset of the bloom occurred in late May to early June in AW, the number of females in early June had already declined by nearly 90% which can largely be attributed to high mortality after prolonged spawning (Diel and Tande, 1992). The decline may also be partially attributed to predation pressure. Herring arrive to the study area in May, showing high feeding activity in May and June (Gislason and Astthorsson, 2002), with a preference of larger copepodite stages (Dalpadado et al., 2000) which attributes to reduce zooplankton abundance (Gislason and Astthorsson, 2002). Kaartvedt (2000) also heuristically suggests that planktivorous fish may influence the timing of descent as a result of reduced predator-prey interactions.

Continuously low EPR, owing to a reduced number of females who also are less active, contribute to a prolonged reproduction in AW during summertime compared to the subarctic waters north of the IFF. Our data showed that several factors could affect the lower spawning frequency, including reduced gut fullness (Fig. 8d) and reduced female size in June and July compared to April and May in AW (Fig. 7). The size reduction does indicate that the females belong to the G_1 generation, which further leads to the question if a portion of the females may not jet at that time have reached reproductive maturity. In June and July, a portion of females are accumulating fat rather than investing the energy to egg production eggs (Fig. 10), which also lowers the EPR.

4.4 Seasonal progression in abundance and composition between water masses

The duration of the development of nauplii and copepodite stages is temperature dependent (Corkett et al., 1986). Using the Belehrádek function provided by Corkett et al. (1986) and the mean local temperature south (~ 8.2 °C) and north (~ 4.0 °C) of the IFF, it would take around three weeks to mature from an egg to stage C1 in AW and around five weeks in SAW. This means that the eggs produced in SAW at the peak of production in late April (Fig. 8e) would be the peak appearing as stage C1 in June (Fig. 5c). The decreased egg production rates in May are reflected in the decrease of C1 abundance in July. Thus, the reproductive pattern is reflected in the abundance and composition in SAW. This is not the case in the AW where despite an increase in female abundance (Fig. 6a) and egg production from April to May (Fig. 8a) a peaked abundance of young copepodite stages in June is not observed. This inconsistency in AW may be due to increased egg cannibalism by copepodite stage C5 and adults, which are increased during a pre-bloom period (Ohman and Hirche, 2001). A change in advection pattern from the downstream area may also result in inconsistencies that we observe south of the IFF.

When comparing the abundances and composition of stages in the AW and SAW within the upper 50 m, slower development within the subarctic waters is apparent in June and July where the proportion of younger individuals is higher. Using the Belehrádek function provided by Corkett et al. (1986) and the mean local temperature north and south of the IFF, it can be calculated that the life cycle of the copepods from egg to stage C5 from the peak spawning in SAW and AW, is completed around early July and late June, respectively. Judging by the increase in abundance in stage C1 in August the previous year, suggests that a

portion of the C5 moult into adults and produce a G_2 in both regions. This contrasts observations made by Strand et al. (2020 and references herein) who were only able to see a G_2 within the Atlantic Water in the Norwegian Sea. Within the Iceland Sea, one generation is observed (Astthorsson and Gislason, 2003).

The observed phenology of two generations within a seasonal cycle north of the IFF appears to be highly dependent upon the eastward extent of subarctic waters from the Iceland Sea. A study by Gaard (1999) shows that the subarctic region at Section N was dominated by the older developmental stages in August 1993, which is a year of increased eastward extension of subarctic waters from the Iceland Sea. In contrast, since 2003 when the eastward extension was reduced, the numbers of stage C1 to C3 have increased in August, north of the IFF (Kristiansen et al., 2019). In recent years, the eastward extension of subarctic waters from the Iceland Sea has increased again (Skagseth et al., in prep) and it appears that the abundance and composition in August, north of the IFF, has reversed to similar phenology as prior 2002 (Kristiansen, unpublished data). Studies along Section N conducted in 2002 showed that the gonad development was at a more advanced stage in AW compared to SAW in May (Gaard, 2002), which agrees with the later onset of reproduction in the Iceland Sea (Gislason, 2018) and earlier onset in AW south of the Iceland Faroe Ridge (Jónasdóttir et al., 2008). This points toward an interchangeable phenology pattern in SAW, depending on the eastward extent of subarctic waters from the Iceland Sea.

4.4.1 Prey availability for pelagic fish

Previous studies have shown that herring tune their feeding migrations to the timing and abundance of the ascended G_0 *C. finmarchicus* populations (Østvedt, 1965; Gislason and Astthorsson, 2002; Broms et al., 2012). Therefore, the years when the inflow from the Iceland Sea is weakened, the herring will find smaller individuals from the G_1 dominating with lower biomass than in years with a high inflow of subarctic water from the west. The subsequent arrival of younger and smaller herring (ICES, 2018) coincides with improved feeding conditions as the G_1 population has advanced to stages C4 and C5 and significantly increased in numbers and biomass from May to June (Fig. 6), both north and south of the IFF. Mackerel arrives later to the feeding grounds than herring. Being less size selective, mackerel exploits the copepod generation available (Kaartvedt, 2000). The earlier onset of *C. finmarchicus* reproduction in SAW leads to an increased abundance of stage C4 and C5 upon the arrival of mackerel in early summer and the presence of a secondary production in late summer (Fig. 6). Thus, the years with a reduced arctic inflow from the west appear to be an advantage for mackerel as food availability has both increased and been extended in time.

5.0 Summary

The present study contains two different *Calanus* populations, separated by the Iceland-Faroe Front (IFF). Ascent occurred earlier but over a prolonged period in the Atlantic Water (AW) south of the IFF compared to the subarctic Water (SAW), dominating north of the IFF. The

population displayed similar composition of developmental stages, with two generations being produced in both regions. The egg reproduction per capita was significantly higher north of the IFF and peaked a month earlier compared to south of the IFF. In contrast, the egg production rates were sustained over a prolonged period in the south. Descent, largely comprised by copepodite stage C4 and C5, was already initiated in June in both regions and coincided with increased accumulated lipid content in late summer.

Acknowledgments

We thank the crew onboard R/V Magnus Heinason and laboratory technicians at FAMRI and DTU Aqua for assistance in collecting and analysing samples and are grateful for the help and constructive comments from co-workers and reviewers. This work is a part of a PhD program in ecology of *C. finmarchicus* in relation to environmental conditions in the south-western Norwegian Sea. The project was funded by the Danish government through the research program "Changes in marine climatic and oceanographic conditions in the waters between the Faroes and Greenland, and their effects on plankton and fish".

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Figures

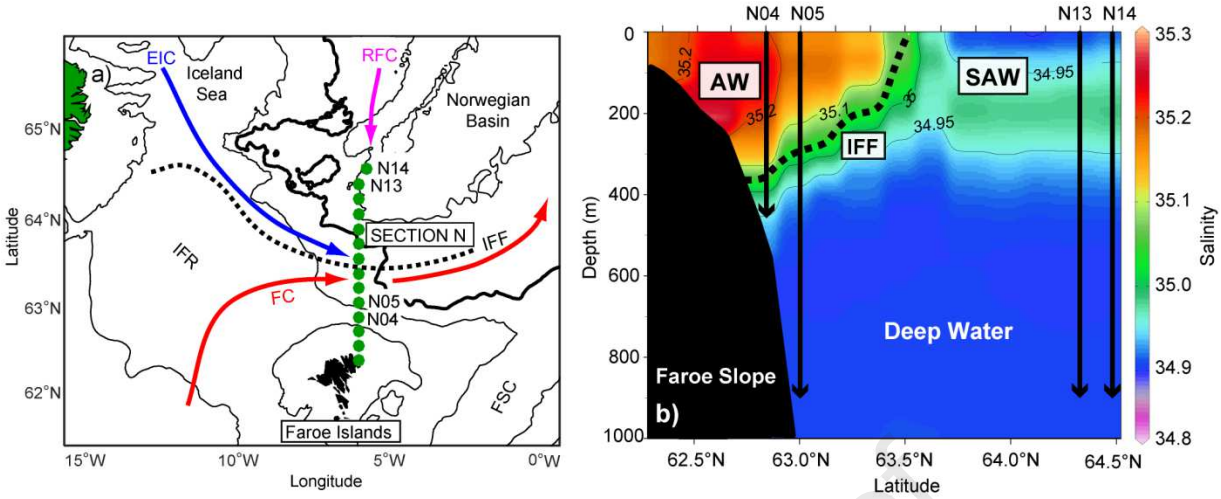

Fig. 1. Map of the study area. The main warm (red) and cold (blue) currents within the upper layers that influence Section N (green dotted line) are displayed (a). The average salinity profile of the water masses along Section N are shown in (b), together with the position of the sampling stations (downward arrows). The salinity average is from February, May and August/September at each station from 2004 to 2019. The Iceland Faroe Front (IFF) is illustrated with a black dotted line in both panels. Abbreviations: FC (Faroe Current), EIC (East Icelandic Current), RFC (Recirculated Faroe Current), IFR (Iceland Faroe Ridge), FSC (Faroe Shetland Channel), AW (Atlantic Water) and SAW (Subarctic Water).

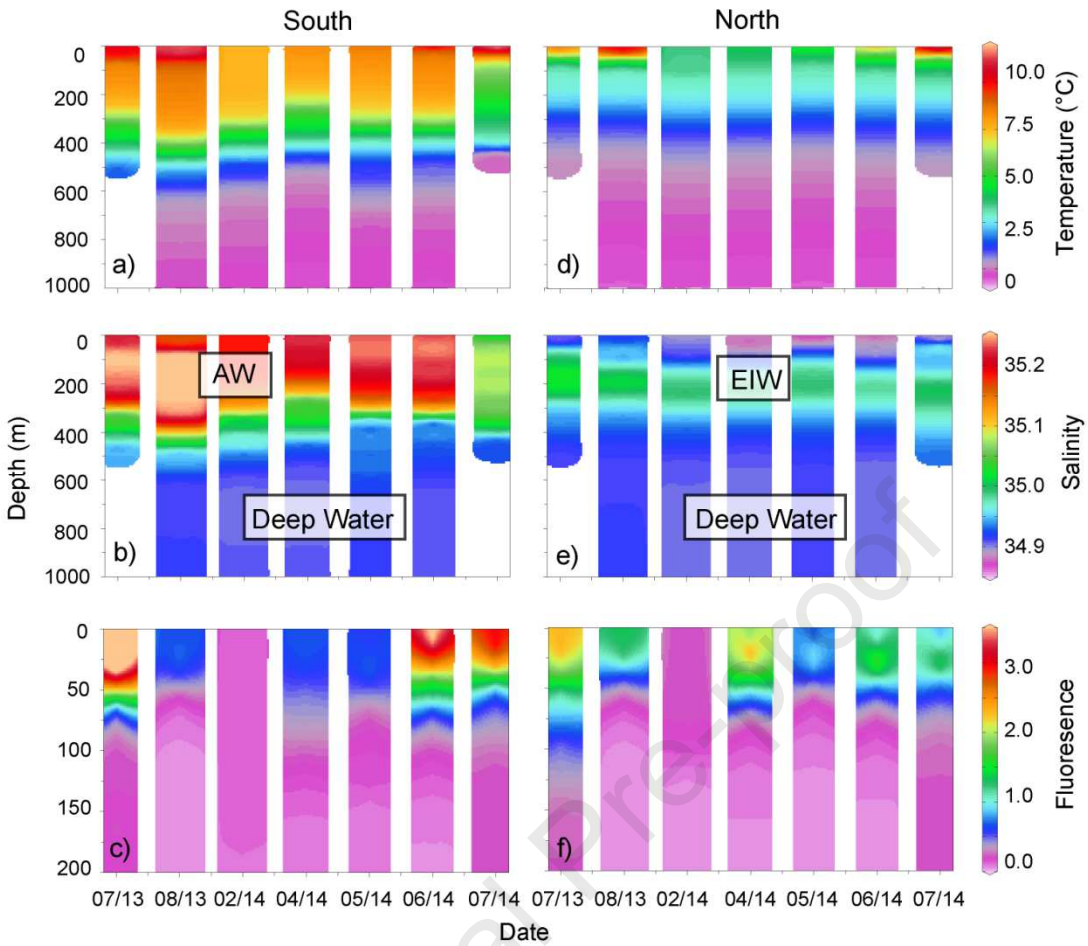

Fig. 2. Vertical profiles of mean temperature, salinity and fluorescence at Section N from seven cruises between July 2013 to July 2014. Averages are from stations N04 and N05, located in south of the IFF (see Fig. 1a) and stations N13 and N14, located north of the IFF. Abbreviations: AW (Atlantic Water) and EIW (East Icelandic Water).

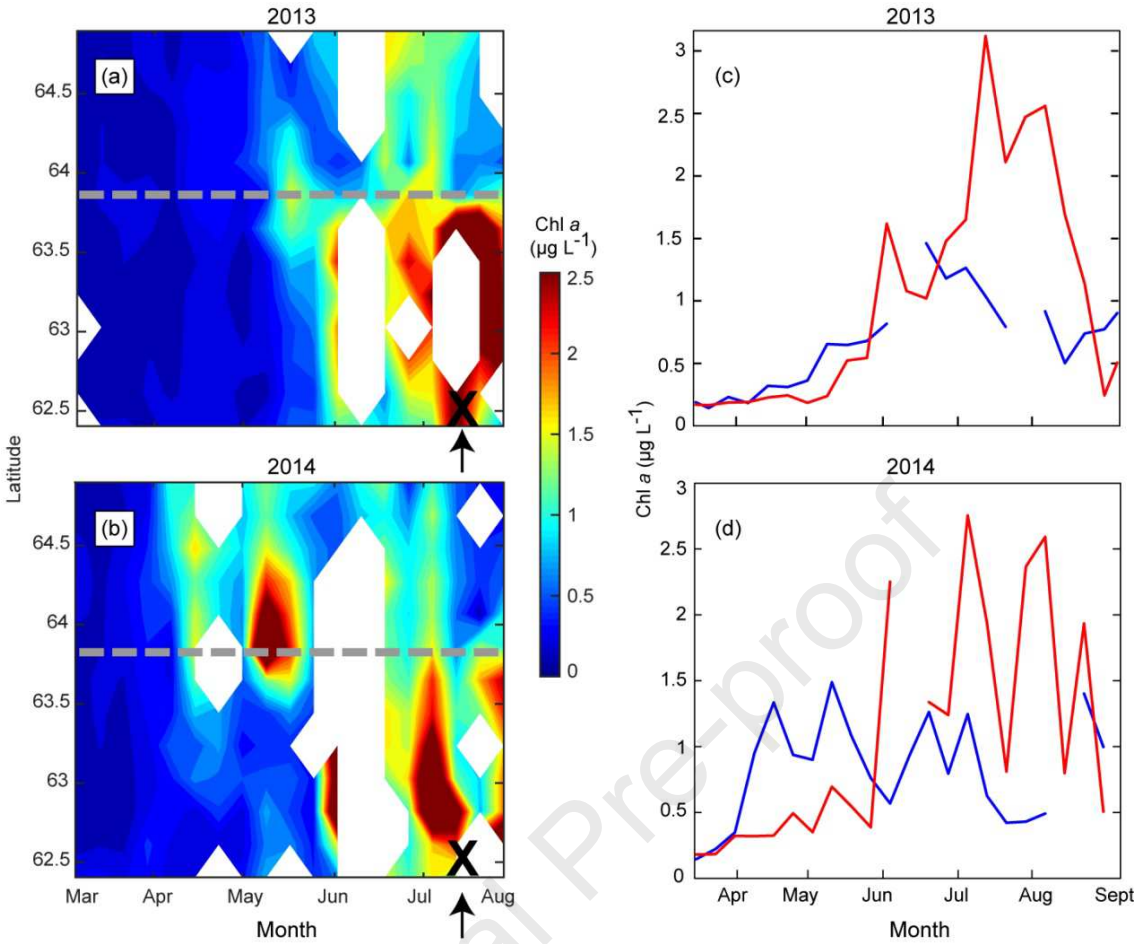

Fig. 3. Hovmöller diagram of satellite-based chl *a* concentration (left panels) and time series of averaged data from the Subarctic Water (SAW, blue line) and Atlantic Water (AW, red line) (right panels) from March 2013 to August 2014. The white spaces in the left panels are data void due to cloud coverage, while the black crosses and arrows indicate the start and finish of the seasonal study. The stippled lines show the position of station N10, which always is north of the IFF (Kristiansen et al., 2016).

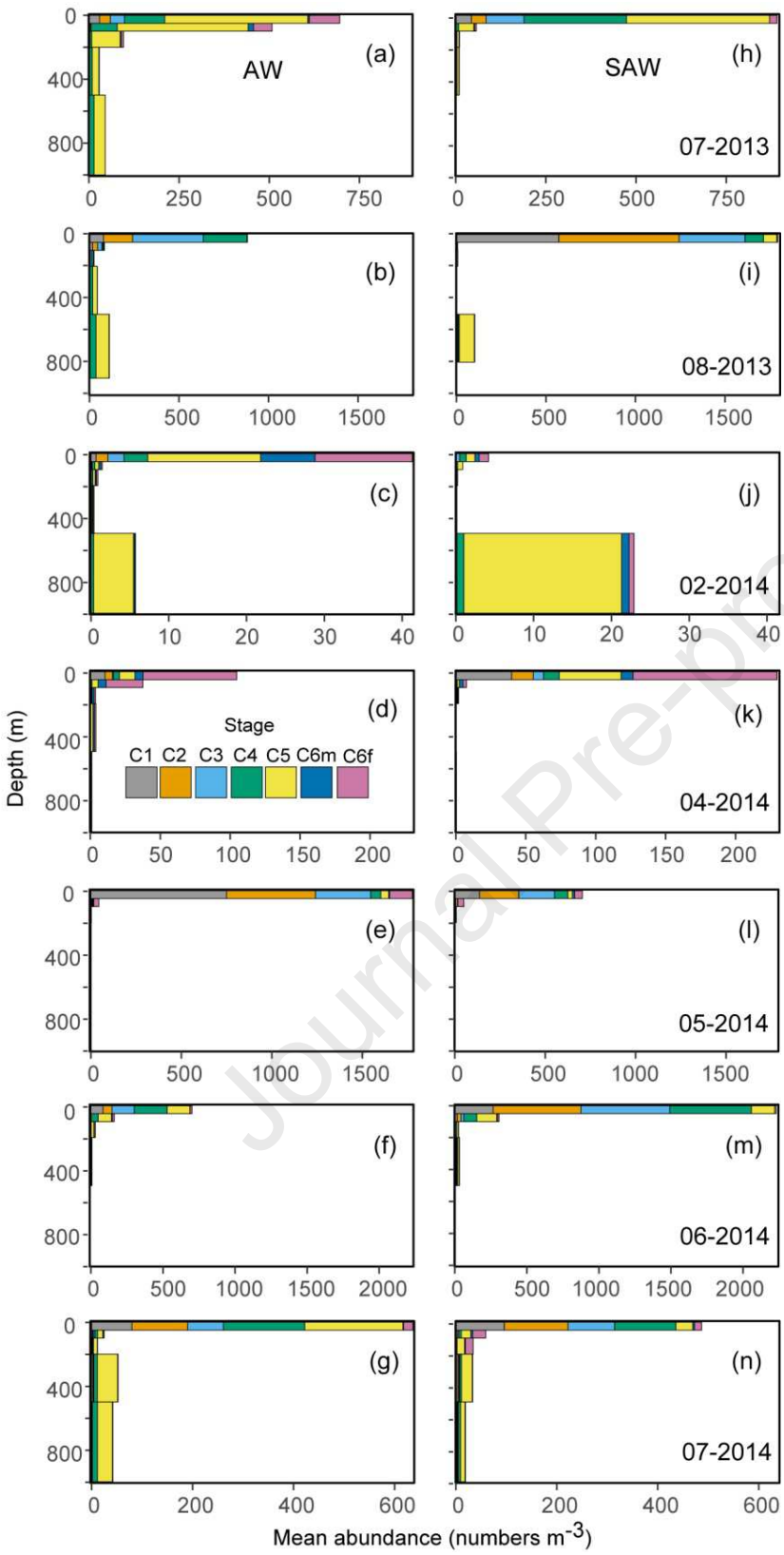

Fig. 4. Seasonal vertical distribution of stage determined *Calanus finmarchicus* from July 2013 to July 2014 in Atlantic Water (AW, south) and Subarctic Water (SAW, north) at Section N. The colour scale represents each copepodite stage by a unique colour. Note that the mean abundance of *C. finmarchicus* is presented in different scales during the sampling season.

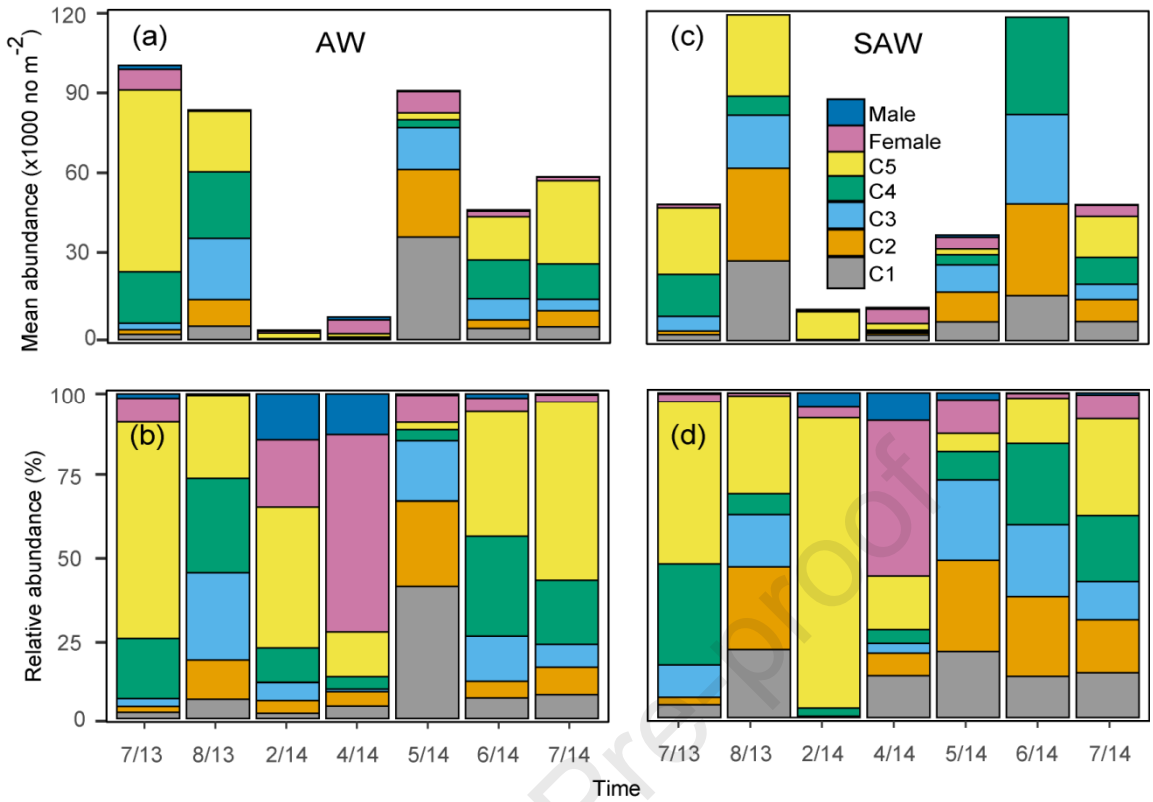

Fig. 5. Total integrated depth (0-1000 m) abundance of *Calanus finmarchicus*. Values are presented in (a) numbers m^{-2} x1000 and (b) relative abundance (%) of each copepodite stage in Atlantic Water (AW, south) and Subarctic Waters (SAW, north) at Section N.

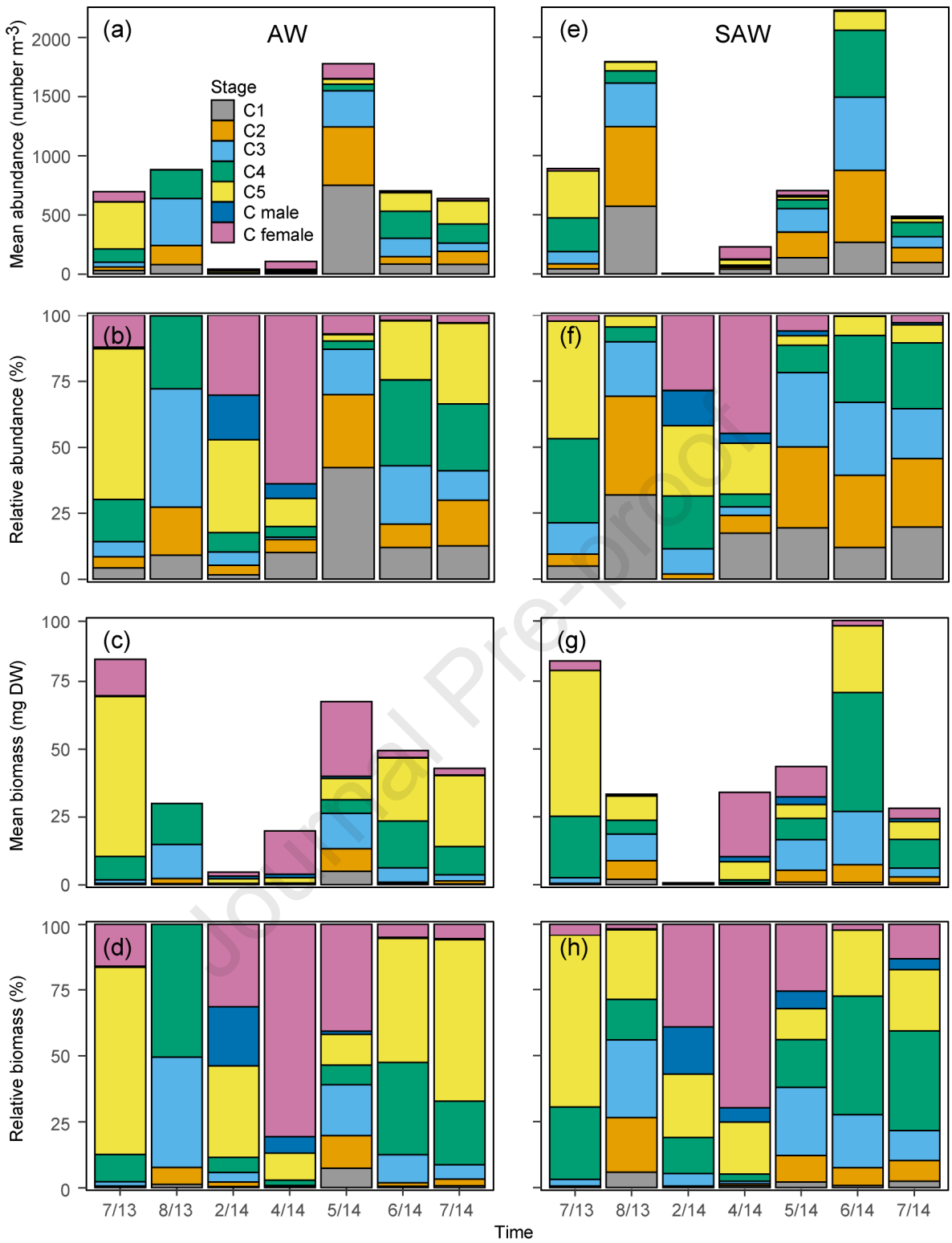

Fig. 6. Seasonal variation of *Calanus finmarchicus* in abundance (numbers m^{-3}) and biomass (mg DW m^{-3}) within the upper 50 m in Atlantic Water (AW, south) and Subarctic Waters (SAW, north) at Section N.

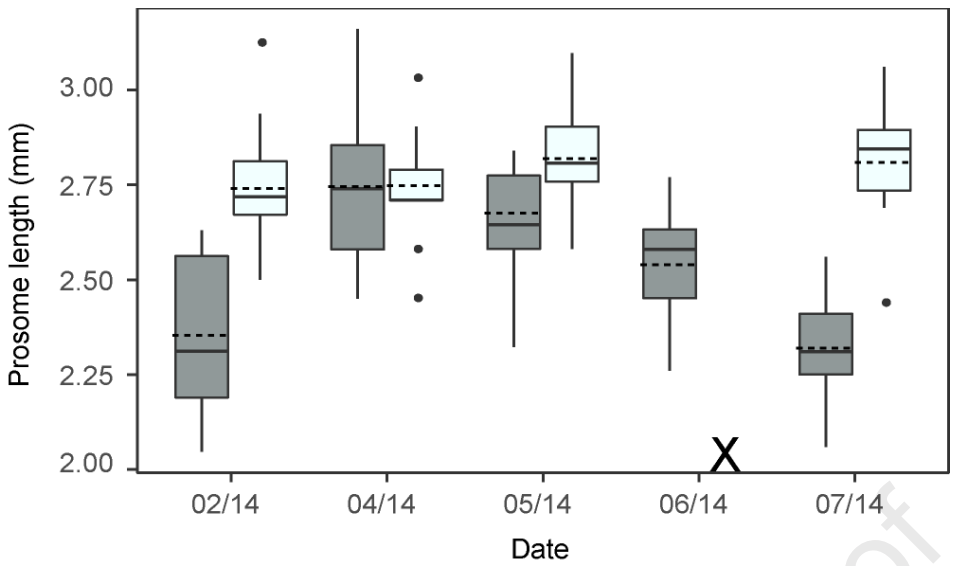

Fig. 7. Seasonal variation in female prosome length in Atlantic Water (AW, grey box) and Subarctic Waters (SAW, white box) within the upper 50 m. The vertical lines show standard error. The solid and dotted horizontal lines represent the median and mean values. The black cross indicates that less than 10 females were found and measured.

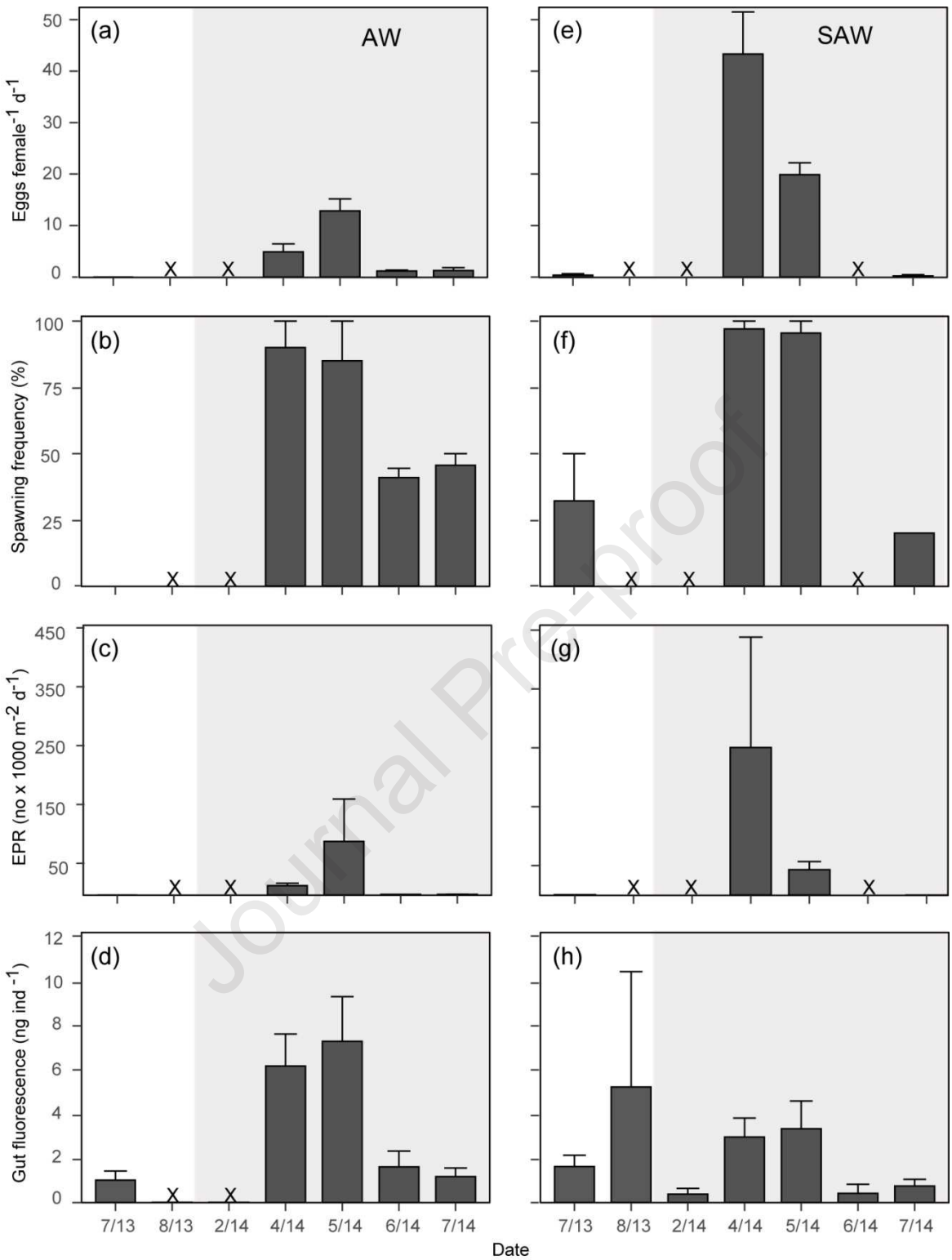

Fig 8. Egg production rates (eggs female^{-1} d^{-1}), spawning frequency (% d^{-1}), population egg production rates (eggs m^{-2} d^{-1} x 1000) and gut chlorophyll content (ng ind^{-1}), as estimated by fluorescence, in *Calanus finmarchicus* females within the upper 50 m of the water column in Atlantic Water (AW, south) and Subarctic Water (SAW, north) at Section N from July 2013 to July 2014. The vertical lines show standard error. The shaded area defines the reproductive period in 2014. Sampling dates where less than five females were caught are indicated by black crosses.

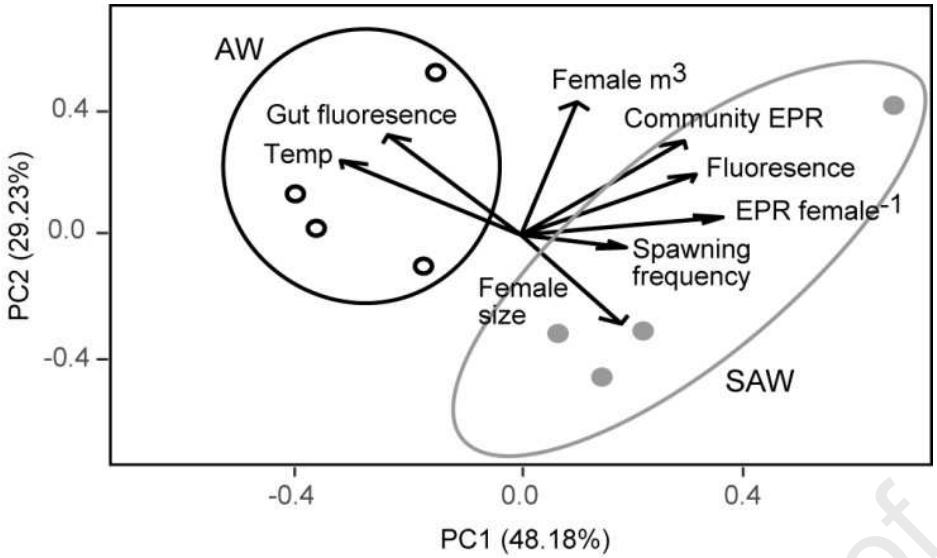

Fig. 9. Ordination biplot, showing the first and second principal component based on a PCA of measured variables that have the potential to influence egg production rates. Direction and length of arrows indicate the direction and rate of steepest increase of the variables. Open (black) and filled (grey) circles denote sampling stations in Atlantic Water and Subarctic Water, respectively. The measured variables are from April and May.

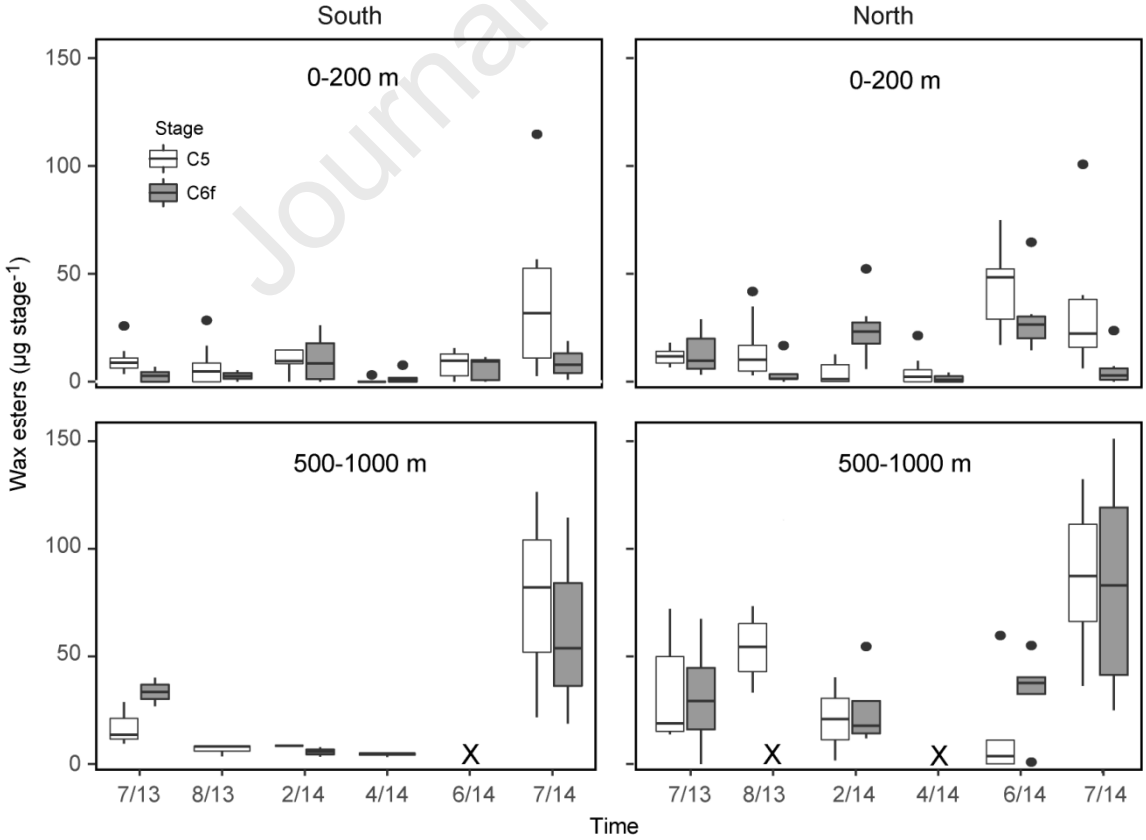

Fig. 10. Wax ester content of *Calanus finmarchicus* stage C5 and females. The box plot shows the median (black line) while the boxes, whiskers and dots show 25/75, 19/90 and 5/95

percentiles respectively. The white boxes represent stage C5 and the grey boxes represent the females (C6f). Sampling dates where less than five individuals were caught are indicated by black crosses.

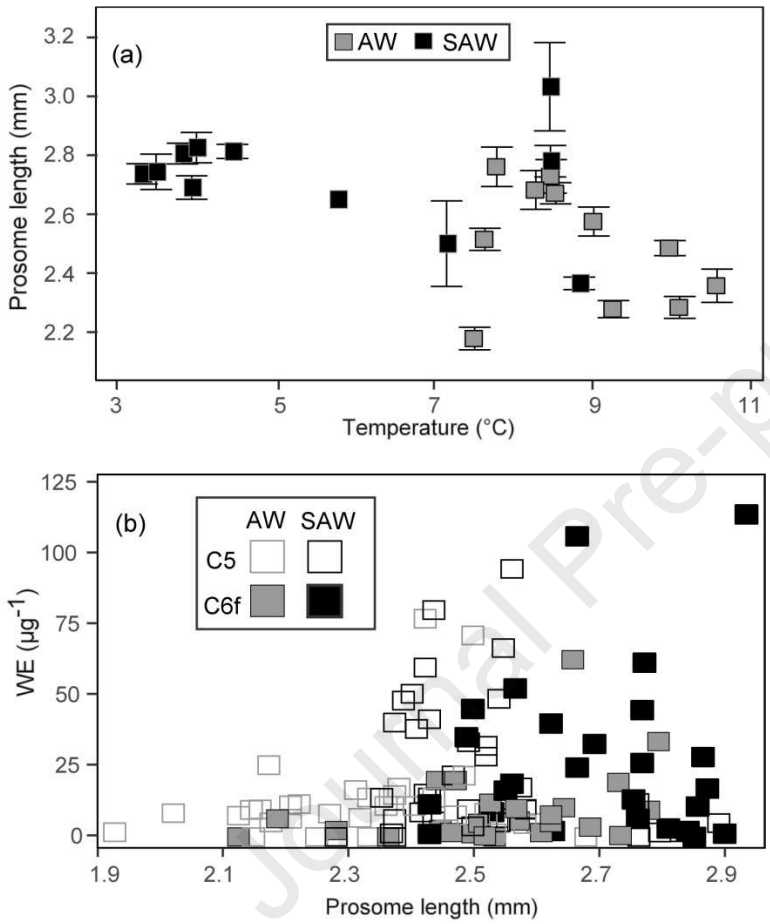

Fig. 11. Size and wax ester (WE) content in relation to temperature throughout the season in Atlantic Water (AW) and Subarctic Water (SAW). (a) Prosome length of females at 0-50 m depth as a function of mean temperature (5-50 m) and (b) wax ester content of copepodite stage C5 and females (C6f) as a function of prosome length. The grey and black squares represent AW and SAW, respectively, at Section N. The vertical lines in (a) show the standard error.

Table 1. Sampling dates and times in Atlantic Water and Subarctic Water throughout the study period.

Atlantic Water			**Subarctic Water**		
Date	Sampling time		Date	Sampling time	
	N4	N5		N13	N14
10.07.13	09.15	11.45	13.07.13	21.45	23.45
29.08.13	04.45	07.30	30.08.13	01.45	06.15
17.02.14	05.30	11.15	18.02.14	08.15	13.45
25.04.14	00.15	03.45	25.04.14	15.00	20.30
12.05.14	04.30	01.00	11.05.14	06.45	03.15
06.06.14	23.00	06.45	06.06.14	16.45	20.30
16.07.14	21.30	23.30	20.07.14	10.15	12.30

Highlights

- *C. finmarchicus* ascend earlier in warm Atlantic Water than in cold Subarctic Water
- Females show increased egg production capacity within the subarctic region
- Increased female size and better feeding conditions are seen in the subarctic region
- Initiation of descent was observed as early as in June in both regions
- Descended individuals had higher lipid content than individuals at the surface

Declaration of interests

X The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: