# Seasonal and interannual variability in abundance and population development of *Calanus finmarchicus* at the western entrance to the Barents Sea, 1995–2019

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## ABSTRACT

Data on copepodid abundance and stage composition of *Calanus finmarchicus* was collected with seasonal resolution (5–6 times a year) from four stations along an oceanographic transect across the western Barents Sea Opening over 25 years (1995–2019). The stations were located in the Norwegian Coastal Current (NCC), inflowing Atlantic water (two stations), and near the Arctic polar front south of Bear Island. Mean copepodite abundance in the water column for the four stations increased from a level around 1000–10,000 individuals m$^{-2}$ in winter to 30,000–100,000 individuals m$^{-2}$ in summer (maximum 670,000 m$^{-2}$). The overwintering (G0) population was dominated by copepodite stage 5 (CV) (40–70%) but with a relatively high fraction also of stage CIV (25–35%) in January. During winter, there was a progressive development of CVs into adult males and females, with mean abundances from 1500 to 4000 adult females m$^{-2}$ in April and May for the stations in the NCC and Atlantic water. Young copepodids of the new spring generation (G1) appeared with relatively high abundances in April at the NCC station and in May at the Atlantic water stations. The data showed a gradient of later development from south to north, reflected both in the maturation of the overwintering generation and in the development of the spring generation. Back-calculations based on temperature-dependent development time suggested peak spawning around late April to mid-May for the Atlantic water stations, and a month or so earlier (in March) for the NCC station, during an early phase of the spring phytoplankton growth. The spring generation developed as a distinct cohort but with large interannual variability in numbers. In Atlantic water, the composition of the copepodid developmental stages in August resembled the situation in June, although it was slightly more advanced. This is interpreted to reflect development of a second generation (G2) spawned upstream sometime in June or early July. The June data suggests that only a small fraction of the G1 cohort develops into adults that spawn and form the G2. There was a tendency of increased summer abundance of *C. finmarchicus* in the inflow region of the southwestern Barents Sea after about 2005. This may be related to the wind regime with more eastward wind-stress at the Barents Sea opening in recent 'high *Calanus*' years compared to 'low *Calanus*' years in the early 2000s.

## 1. Introduction

*Calanus finmarchicus* is a boreal zooplankton species distributed in the North Atlantic in waters with mean annual temperatures of about 5–10 °C (Conover, 1988; Planque and Fromentin, 1996; Planque and Batten, 2000; Helaouët and Beaugrand, 2007; Helaouët et al., 2011). It occurs with highest population abundance in two core areas in the subarctic gyres in the Norwegian Sea and the Labrador Sea (Sundby,

2000; Helaouët et al., 2011; Reygondeau and Beaugrand, 2011; Melle et al., 2014). From the Norwegian Sea the distribution extends into the southern Barents Sea where it is the dominant mesozooplankton species (Tande, 1991; Melle and Skjoldal, 1998; Falk-Petersen et al., 2009; Aarflot et al., 2018). Here it is found in comparatively warm Atlantic water (about 3–8 °C) associated with the inflowing currents from the adjacent Norwegian Sea (Fig. 1). As this water cools (to near 0 °C) on its way through the eastern Barents Sea towards the exit between Novaya

Zemlya and Franz Joseph Land, the conditions for reproduction become suboptimal and *Calanus finmarchicus* is considered expatriated in the cold water masses of the northern Barents Sea (Jaschnov, 1970; Tande et al., 1985; Melle and Skjoldal, 1998; Hirche and Kosobokova, 2007; Skaret et al., 2014).

The *Calanus finmarchicus* population in the Barents Sea depends on the supply of individuals with inflowing water from the Norwegian Sea (Skjoldal and Rey, 1989; Skjoldal et al., 1992; Tande and Slagstad, 1992; Dalpadado et al., 2012, 2014; Hunt et al., 2013; Skaret et al., 2014). This flow across the opening between mainland Norway and Bear Island consists of two main current components: a branch of Atlantic water (the North Cape Current) from the Norwegian Atlantic Current, and the more southerly situated Norwegian Coastal Current (NCC) along the Norwegian coast (Fig. 1; Skagseth et al., 2008, 2011). The current structure across the Barents Sea Opening can be complex with some recirculation and outflow of water in the northern part of the opening south of Bear Island (Ingvaldsen, 2005; Skagseth, 2008). There is also strong temporal

variation on seasonal and interannual scales, with currents responding to local wind and atmospheric pressure conditions (Ådlandsvik and Loeng, 1991; Ingvaldsen et al., 2004a, 2004b, Skagseth et al., 2008; Lien et al., 2013b).

In addition to variability in the currents, the influx of *Calanus finmarchicus* also depends on the abundance and vertical distribution of individuals upstream in the adjacent Norwegian Sea. The overwintering population of *C. finmarchicus* resides deep (>500 m) in the cold waters of the Norwegian Sea (Østvedt, 1955; Halvorsen et al., 2003; Heath et al., 2004; Melle et al., 2004, 2014; Edvardsen et al., 2006). Only after ascending in late winter to spawn and develop as new generations in the upper water layer, do they become available for transport with the currents into the Barents Sea. This results in a strong seasonality with low influx in winter and high influx in summer, which is expected to result in a spatial pattern of low abundance of *Calanus finmarchicus* in advected 'winter water' and high abundance in 'summer water' inside the Barents Sea (Skjoldal and Rey, 1989; Skjoldal et al., 1992; Blindheim
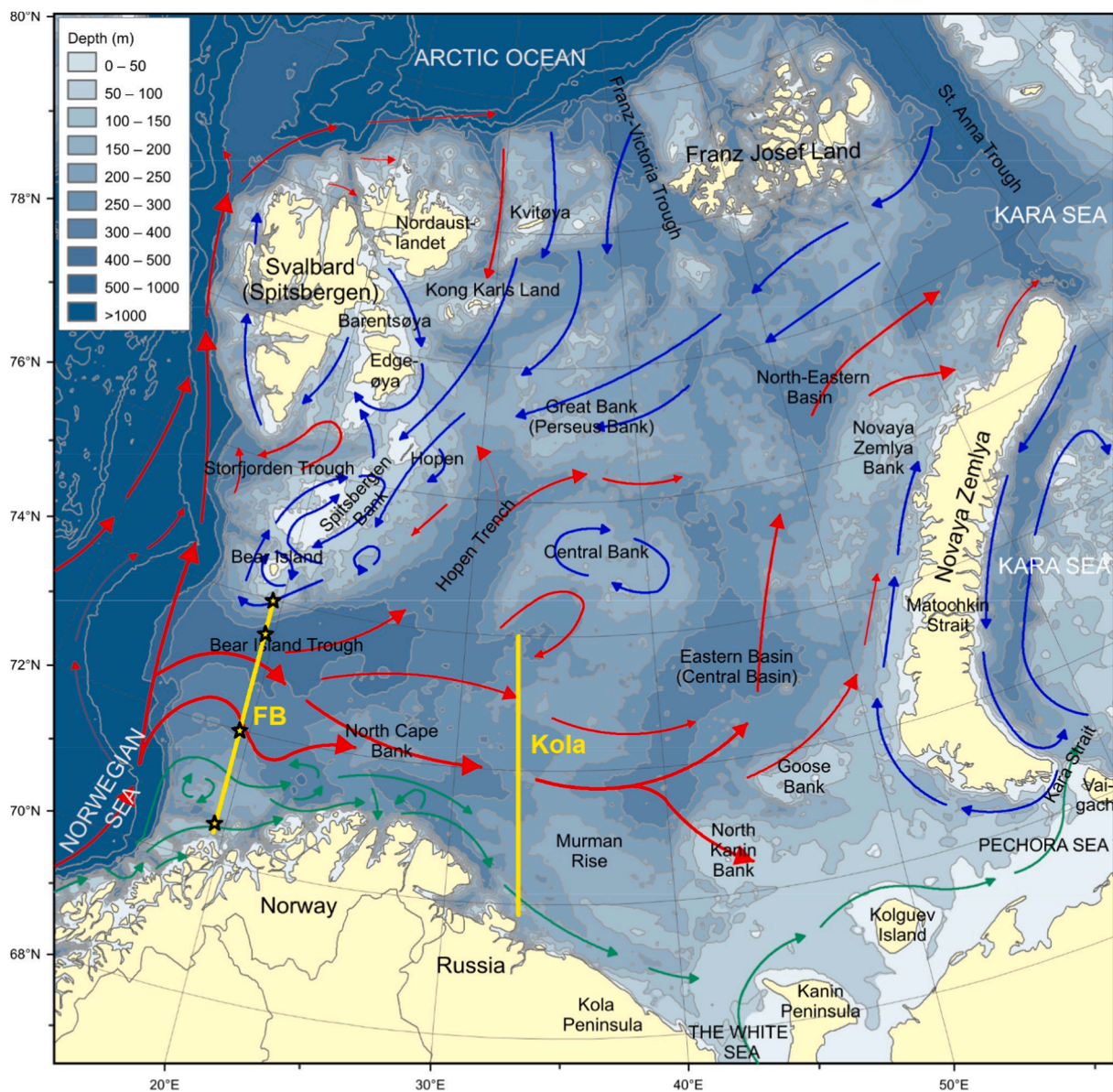


**Fig. 1.** Map of Barents Sea showing the location of the Fugløya-Bjørnøya (Bear Island) transect across the Barents Sea opening with the locations of the four sampling stations shown by star symbols. Arrows show schematic ocean currents with the Norwegian Coastal Current (green), branches of Atlantic water flows (red), and flows of Arctic water (blue). Also shown is the location of the Russian Kola transect. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

and Skjoldal, 1993). Russian investigations (from 1959 to 1992) in spring and summer indicated a clear pattern of elevated zooplankton biomass in the branches of Atlantic water flowing into the southwestern Barents Sea (Degtereva, 1979; Bliznichenko et al., 1984; Degtereva et al., 1985, 1986a, 1986b).

*Calanus finmarchicus* has an annual life cycle with one generation per year in the main areas of its distribution (Østvedt, 1955; Conover, 1988; Tande, 1991; Heath et al., 2008; Broms et al., 2009; Bagøien et al., 2012; Melle et al., 2014). In warmer water in the southern part of its range, it can have two or even more generations per year, such as in the Clyde Sea area (Irish Sea) shown in the pioneering and classical studies by Marshall and Orr (1955, 1972). Two generations have been reported from studies in Norwegian coastal waters south of the Lofoten area (Sømme, 1934; Wiborg, 1954; Matthews et al., 1978), while only one generation has been found in fjords inside the Barents Sea (Tande, 1991; Diel and Tande, 1992). Previous studies from the Barents Sea have suggested that there is only one distinct cohort developing from spawning in spring each year (Jaschnov, 1970, 1972; Skjoldal et al., 1987; Tande, 1991; Tande and Slagstad, 1992; Melle and Skjoldal, 1998). However, a modelling study suggested that two generations per year are likely in the warmer Atlantic water in the southern Barents Sea (Skaret et al., 2014). Gluchowska et al. (2017) interpreted observations from the West-Spitsbergen Current to show a possible second generation. A recent study at the western entrance to the Barents Sea based on the Continuous Plankton Recorder Survey (near-surface data) for the years 2008–2016 also indicated a second generation (Strand et al., 2020).

The spring generation (G1) of *Calanus finmarchicus* stems from spawning by the overwintering generation (G0) at the time of the spring phytoplankton bloom. Egg production by females depends to a large extent on external food (as opposed to internal reserves), and spawning of G0 females has been found to be related to the seasonal build-up of chlorophyll *a* in the early part of the spring phytoplankton growth in Atlantic water in the Barents Sea as well as in the Norwegian Sea (Marshall and Orr, 1972; Diel and Tande, 1992; Hirche, 1996; Melle and Skjoldal, 1998; Niehoff et al., 1999; Harris et al., 2000; Melle et al., 2004, 2014; Niehoff, 2007). The spring phytoplankton bloom in Atlantic water is driven by stabilization from the seasonal warming and thermocline formation (Skjoldal and Rey, 1989; Olsen et al., 2003; Dalpadado et al., 2020). The seasonal warming in spring, through the effect on phytoplankton, influences the timing of reproduction of *C. finmarchicus* and acts to synchronize the G1 cohort development to that of the phytoplankton spring bloom (Melle and Skjoldal, 1998). Temperature has also a direct influence on the rate of development of the new generation (Corkett et al., 1986; McLaren et al., 1989; Campbell et al., 2001).

The Institute of Marine Research (IMR) in Norway operates an oceanographic transect running South to North across the Barents Sea Opening between mainland Norway (at Fugløya) and Bear Island (Fig. 1). The Fugløya-Bear Island transect (hereafter FB transect) has been operated since 1964 with sampling 5–6 times per year since 1977 (Ingvaldsen et al., 2003). Hydrography, nutrients, chlorophyll *a*, and zooplankton have been monitored along the FB transect since the early 1990s. Here we report on a 25-year time series (1995–2019) on *Calanus finmarchicus* in this inflow region to the Barents Sea. We present data on abundance and stage composition of copepodites and address the issue of seasonal cohort development. We also examine the evidence for one or two generations per year at different locations and water masses along the transect. During the period covered by this study there has been warming of the Barents Sea by more than 1 °C in the inflowing Atlantic water (Dalpadado et al., 2014, 2020; Eriksen et al., 2017; Skagseth et al., 2020). We examine whether there has been a change in cohort structure and abundance of *C. finmarchicus* related to the warming, which has been associated with on-going 'borealization' of the Barents Sea (Fossheim et al., 2015; WGIBAR, 2020).

## 2. Materials and methods

### 2.1. Sampling

We have examined samples from four stations located at latitudes 70.5, 72, 73.5 and 74°N along the FB transect (Fig. 1). The southernmost station (70.5°N) is situated in the NCC at a water depth of about 140 m and with salinities generally < 34.6 (Fig. 2). The stations at 72 and 73.5°N are located in Atlantic water at the northern flank of 'Tromsø-flaket' and in the deepest part of the Bear Island Channel at depths of about 310 m and 480 m, respectively. The northernmost station at 74°N is located at the slope south of Bear Island at a water depth of about 140 m in the frontal area between Atlantic water and the colder and less saline Arctic water of the Bear Island Current.

The FB transect has generally been covered 5–6 times each year: January, March, April, June, August, and October. Additional sampling has been made in May some years. The autumn sampling in October was moved about one month later to November after 2012. Due to practical constraints regarding the annual IMR cruise plans, there has been some variation in timing of the seasonal coverage among years, and there are also some gaps in the time series (Fig. 3). While some zooplankton samples were collected at the FB transect from 1990, regular sampling with seasonal resolution started in 1995, which is the first year of the time series we report here.

Zooplankton samples were collected using vertical hauls from near the bottom to the surface with a WP-2 net (56-cm diameter, 180 μm mesh; Skjoldal et al., 2019). The net was used without flowmeter, and the volume filtered was calculated from tow length and area opening of the net.

Salinity and temperature measurements were obtained with SeaBird SBE 911 + Conductivity-Temperature-Depth (CTD) systems on the IMR research vessels. The accuracy of the temperature and conductivity sensors are 0.0002 °C and 0.0002 S/m, respectively. Furthermore, the salinity measurements from each cruise have been calibrated against water samples, and the temperature and conductivity sensors are calibrated annually. Samples for nutrients and chlorophyll *a* were collected with a rosette of Niskin water bottles mounted on the CTD and analyzed as described in Dalpadado et al. (2020).

### 2.2. Analysis of zooplankton samples

Sample treatment followed the standard IMR procedure which includes splitting the sample in two halves, one used for determination of dry weight biomass in three size fractions, and the other fixed with buffered (borax) 4% formaldehyde solution in sea water and stored for later taxonomic analysis (see Melle et al., 2004; Skjoldal et al., 2013 for further details). The latter includes adaptive subsampling according to the numerical density of taxa; large individuals are commonly counted in the whole sample, while small individuals of more abundant taxa are counted in a fraction of the sample (Hassel et al., 2017). In our case, copepodites of *Calanus* species were usually counted in 1/16, 1/32 or 1/64 fractions of samples when they were abundant in spring and summer; occasionally counts were made for 1/128 or 1/256 fractions for samples with particularly high abundances. Larger fractions were analyzed for winter samples when copepodite abundance was low, typically ranging from the whole sample down to 1/16 sample fraction. Older and larger copepodite stages were often counted in larger fractions than more abundant younger and smaller copepodite stages. Subsampling introduces additional variance to abundance estimates (Van Guelpen et al., 1982; Skjoldal et al., 2013) but is a practical necessity.

Four species of *Calanus* were identified in the samples from FB; in addition to *Calanus finmarchicus* these were *C. glacialis*, *C. hyperboreus* and *C. helgolandicus*. The species were identified and distinguished from each other based on size (cephalothorax length) and morphological criteria. Size-limits for separation of the various copepodite stages of *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus* have been determined
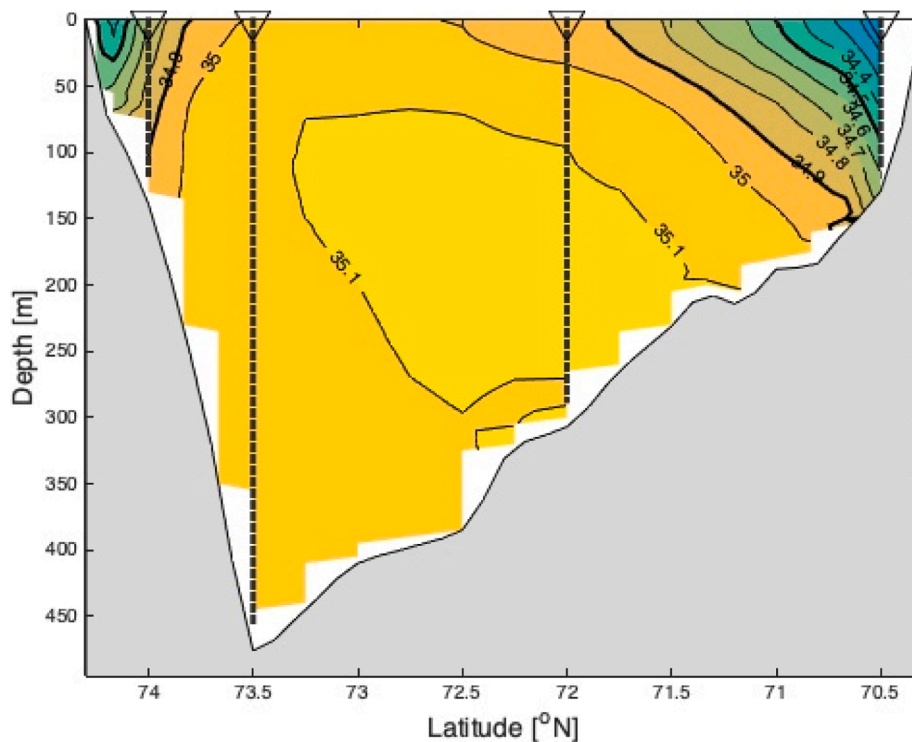
**Fig. 2.** Water depth and mean summer salinity distribution (June–September 1995–2015) across the Fugløya-Bear Island hydrographic section from mainland Norway (right) to Bear Island in north (left). Triangles and vertical lines show the locations of the four sampling stations.
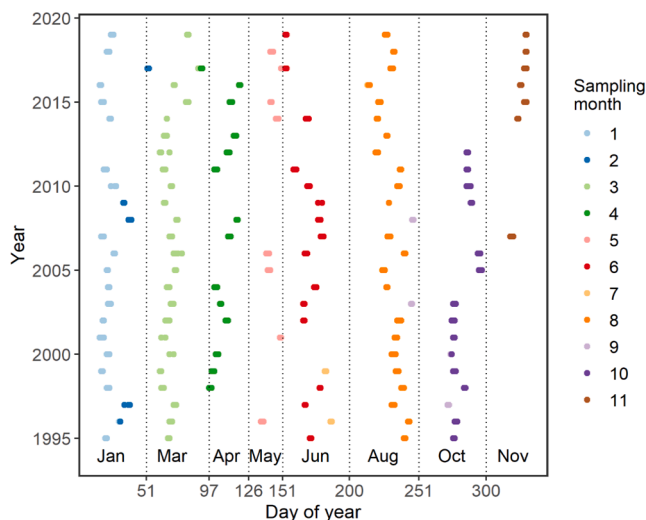


**Fig. 3.** Sampling time (Julian day number) for the sampling periods (separated by vertical lines) from January to November 1995–2019. The January sample series is from the late part of January extending into early February in some years (17 January-9 February). The March series is from 21 February to 7 April, the April series from 7 to 29 April, the May series (only 6 years) from 14 to 30 May, the June series from 2 June to 5 July, the August series from 31 July to 3 September, the October series from 29 September to 24 October, and the November series from 14 to 26 November.

empirically based on samples from the Barents Sea (Tande et al., 1985; Hassel, 1986; Melle and Skjoldal, 1998). *C. hyperboreus* is the largest species and is usually clearly distinguished by its size. There is some stage-specific overlap between small individuals of *C. glacialis* and large individuals of *C. finmarchicus*, which can represent up to about 30% of individuals in the southern range of *C. glacialis* (Grainger, 1961; Hassel, 1986; Parent et al., 2011; Gabrielsen et al., 2012). Individuals of

intermediate size of stage CV and adult females were inspected for curvature and structure of the coxopodites of the 5th pair of legs (Jaschnov, 1955, 1972; Frost, 1974) to help distinguish the two species. We note that this criterion is variable and only partially effective in separating the two species (Choquet et al., 2018).

*Calanus helgolandicus* is of similar size as *C. finmarchicus,* and the two species were separated on basis of the curvature of the coxopodites of the 5th leg pair and shape of the head (Fleminger and Hulseman, 1977). As routine, 20 individuals (if available) of both CV and adult females were examined to determine the species' proportions. Younger copepodite stages were not separated, but *C. helgolandicus* was assumed to be scarce as judged from the low proportions of the older stages. *C. helgolandicus* is a more southerly species with a spawning period later in the season than *C. finmarchicus* (Planque and Fromentin, 1996; Bonnet et al., 2005).

### 2.3. Copepodite stage composition of Calanus finmarchicus

To explore seasonal development of generations, a mean copepodite stage index (CSI) was calculated as an abundance weighted average:

$$CSI = \frac{\sum i \times n_i}{\sum n_i}$$

where $i$ is copepodite stage number from 1 to 6, $n_i$ is abundance of stage $i$, and summations are for $i$ from 1 to 6. The CSI varies from 1 (all CI) to 6 (all adults) and reflects the stage composition of the population with new cohorts recognized by low index values.

The female/CV index of Diel and Tande (1992) (females - CV)/(females + CV) was used to characterize the degree of development of adult females in the population. This ratio varies from −1 (all CV) to + 1 (all females) and is 0 when there are equal proportions of females and CVs.

### 2.4. Wind stress

We used information on wind stress to indicate conditions for

transport of *Calanus finmarchicus* into the Barents Sea as well as data from an ocean model. Wind stress data were obtained from the ERA-Interim global atmospheric reanalysis (Dee et al., 2011). The original reanalysis had a spatial resolution of the order 80 km, and here we used gridded daily fields at a spatial resolution of 0.25 * 0.25° in latitude and longitude.

### 2.5. Statistical analyses

#### 2.5.1. Correlations

Pearson correlation coefficient (r) was used to describe relationships between *Calanus finmarchicus* and environmental variables. Correlations were used in an exploratory manner to characterize structure of the data sets without implying causality. Abundance of *C. finmarchicus* copepodites were log(10) transformed since they follow an approximate log-normal distribution (not shown).

#### 2.5.2. Environmental effects on copepodite stage composition (CSI)

We used linear regressions to explore the effect of environmental variables (temperature 0–50 m and nitrate 0–20 m) on the stage composition (CSI) of *Calanus finmarchicus* in the June sample-series. Sampling date (day of year) and station (categorical) were included in the analyses, and models were compared using the Akaike selection criteria (AIC; Akaike, 1974). The June series was selected because the new spring generation of *C. finmarchicus* was developing at this time, and the CSI was used to indicate variation in its development.

#### 2.5.3. Seasonal and interannual trends in copepodite abundance

We employed generalised additive models (GAMs) (Hastie and Tibshirani, 1990; Wood, 2006) to assess seasonal and interannual trends in copepodite abundance. Analyses were based on the sum of older *Calanus finmarchicus* individuals belonging to stages CIV, CV, and adults, and restricted to the two stations located in Atlantic water. The older copepodid stages were used since they were dominant on most sampling occasions and considered most representative for the general population level.

The GAMs were run in R (version 3.6.2; R Core Team, 2019) using the mgcv library (Wood, 2017). Abundance (individuals m$^{-2}$) of *C. finmarchicus* (log$_e$ of sum of CIV, CV, and adults) was used as response variable, while Year (1995–2019), Day-in-Year, and sampling station (categorical) were used as predictors. The purpose of including both year and day in year as covariates in the same model was to separate interannual and seasonal effects (c.f. Wood, 2006). Analyses were run both on the full dataset including samples throughout the season and restricted to data from summer months (June + August) only. GAM models allow for non-linearities, and the degree of smoothing was controlled by generalised cross-validation.

The GAM model is given as:

$$\log_e(C.\ \text{finmarchicus}_i) = \alpha + s_1(\text{Day} - \text{in} - \text{Year}) + s_2(\text{Year}) + \text{Station} + \varepsilon_i \tag{1}$$

where $\alpha$ is the intercept, $s_1$ and $s_2$ are smoothing functions, and $\varepsilon_i$ is the residual. When analysing only summer data, the effect of Station (72.0°N versus 73.5°N) was not significant and this term was therefore omitted.

The model was evaluated by scrutinizing the residuals, which were plotted against the fitted values as well as each of the predictor variables. GAMs were run on the residuals versus the predictor variables to check for any consistent patterns. Also, a semivariogram for the model residuals was used to evaluate temporal autocorrelation using the function "variog" in the R package "geoR" (Ribeiro and Diggle, 2018). The variograms were not entirely conclusive, hence the possibility of some autocorrelation remaining in the residuals could not be ruled out, which implies that the *p*-values might be somewhat on the low side.

## 3. Results

### 3.1. Abundance of four Calanus species

*Calanus finmarchicus* was by far the numerically dominant of the four *Calanus* species recorded at the FB transect (Table 1). Copepodite abundance of *C. finmarchicus* in summer was typically around 50,000 individuals m$^{-2}$ with an average over 4 stations and 25 years for June and August of 67,700 individuals m$^{-2}$ (SD 103,700). By comparison the abundance of *C. glacialis* was typically 2 orders of magnitude lower (around 500–1000 individuals m$^{-2}$ with a maximum of 53,500 m$^{-2}$), while the abundance of *C. hyperboreus* was 3 orders of magnitude lower (around 100 individuals m$^{-2}$ with maximum 2300 m$^{-2}$; Table 1). The abundance of *C. finmarchicus* in winter (January-March) was much lower than in summer, typically in the range 1000–10,000 individuals m$^{-2}$ with maximum 45,300 m$^{-2}$. *C. helgolandicus* generally occurred in low abundance, with an overall average of about 30 individuals m$^{-2}$ for CV and adult females (Table 1). The species was present primarily at the NCC station and in the autumn, with a frequency of occurrence of about 30% of the samples over the year. *C. helgolandicus* was less common at the Atlantic water stations (frequency of occurrence about 10%), where its contribution was negligible compared to the numbers of *C. finmarchicus* during spring and summer. However, in autumn and winter (October-March) when *C. finmarchicus* was at its seasonal low, the fraction of *C. helgolandicus* tended to be greater (up to over 50% for adult females in a few cases for the NCC station).

The total abundance of *Calanus finmarchicus* copepodites in summer showed large interannual variation, by two orders of magnitude in range of values, and with coefficients of variation (SD/mean) of 1.1–2.6 (Table 2). This reflected skewed, log-normal-like frequency distributions (not shown) with medians being smaller than the arithmetic means by a factor of about 2. The values at single stations ranged from a low of about 1000 copepodites m$^{-2}$ to a maximum of 672,000 m$^{-2}$. The summer abundance was generally similar at the NCC and Atlantic stations with mean values in the range 50–100,000 copepodites m$^{-2}$ for June and August, while being lower at the northernmost station in June (mean value of about 20,000 copepodites m$^{-2}$; Fig. 4).

### 3.2. Seasonal pattern of copepodite stage composition

In winter, the *Calanus finmarchicus* population was dominated by the main overwintering stage CV as well as a fairly high fraction of stage CIV (30–40% in January at the Atlantic water stations; middle panels in Fig. 4B). The winter abundance was very low at the two southernmost stations (mean values 250–2500 copepodites m$^{-2}$), while being higher at the deepest station (73.5°N; about 5000–20,000 copepodites m$^{-2}$) and partly also at the northernmost station (Fig. 4A). At all stations, there was a progression in development from stage CV into adult females and males from January to April, with a temporal delay from south to north (Fig. 4B). Adult males appeared with maximum relative abundance (up to 10% as average value) in March or April.

Young copepodids were present in January at the NCC station (70.5°N) although at very low absolute abundance (Fig. 4, lower panels). A substantial increase in young copepodids of the new generation was seen at this station in April, with a mean abundance of about 50,000 individuals m$^{-2}$ and CI-CIV making up over 80% of the total copepodids. At the same time (April), there were only some first signs of a new generation with low abundance (<7000 individuals m$^{-2}$) at the Atlantic water stations (Fig. 4, middle panels). By June the situation was very different, with high abundance of the new generation developing in the Atlantic water with mean total abundance of 80–90,000 individuals m$^{-2}$; young stages CI-CIII made up about 50% of the total population while CIV made up another 25–30%. The stage of population development at the northernmost station (74°N) in June appeared similar to that of the northern Atlantic station although the total copepodid abundance was quite a bit lower (mean about 20,000 individuals m$^{-2}$; Fig. 4, top

**Table 1**

Copepodite abundance (individuals m$^{-2}$) of *Calanus finmarchicus*, *C. glacialis*, *C. hyperboreus*, and *C. helgolandicus* along the FB transect during 1995–2019. Mean, median, minimum, and maximum values, and standard deviation (SD), coefficient of variation (CV = SD/mean), and number of observations (*n*) for all samples across the four sampling stations and seasons for each species. Values are also given separately for the winter (January and March), spring (April and May), summer (June and August), and autumn (October and November) periods for *C. finmarchicus*. Note that values for *C. glacialis* and *C. hyperboreus* are given for presence-data only; these species were present in 54% and 47% of the samples, respectively. The values for *C. helgolandicus* are for copepodite stage CV and adult females. Note that *C. helgolandicus* was not separated from *C. finmarchicus* and constituted up to 50% of the lowest counts (of both species combined) in winter. Values are rounded to nearest 10 (for low values) or 100.

| Species | | Mean | Median | Min | Max | SD | CV | n obs. |
|---|---|---|---|---|---|---|---|---|
| *Calanus glacialis* | (presence only) | 1 500 | 260 | 8 | 53 500 | 4 800 | 3.16 | 267 |
| *Calanus hyperboreus* | (presence only) | 240 | 90 | 4 | 2 300 | 360 | 1.49 | 231 |
| *Calanus helgolandicus* | (CV and females) | 32 | 0 | 0 | 2 200 | 160 | 5.04 | 372 |
| *Calanus finmarchicus* | Total | 32 700 | 9 300 | 60 | 671 700 | 69 400 | 2.12 | 496 |
| | Autumn | 21 300 | 9 700 | 270 | 128 500 | 23 300 | 1.09 | 84 |
| | Spring | 34 600 | 9 500 | 220 | 285 700 | 58 100 | 1.68 | 79 |
| | Summer | 66 000 | 28 800 | 950 | 671 700 | 101 800 | 1.54 | 162 |
| | Winter | 4 900 | 2 040 | 60 | 45 300 | 6 807 | 1.38 | 171 |

**Table 2**

Summary statistics (mean, median, minimum, maximum, standard deviation (SD), coefficient of variation (CV), and number of observations n) for total abundance of *Calanus finmarchicus* copepodites (individuals m$^{-2}$) in summer (June and August) at the four sampling stations along the FB transect during 1995–2019. Values are rounded to nearest 10 (for low values) or 100.

| Station | Mean | Median | Min | Max | SD | CV | n obs. |
|---|---|---|---|---|---|---|---|
| 74.0°N | 40 600 | 12 500 | 950 | 671 700 | 105 600 | 2.60 | 41 |
| 73.5°N | 92 900 | 64 000 | 10 900 | 448 500 | 103 200 | 1.11 | 41 |
| 72.0°N | 66 700 | 36 500 | 2 600 | 611 300 | 101 000 | 1.51 | 40 |
| 70.5°N | 70 700 | 26 200 | 1 500 | 491 500 | 102 100 | 1.44 | 40 |

panels).

The population development of *Calanus finmarchicus* in Atlantic water between June and August gives an appearance of being arrested, with the copepodid composition in August resembling that in June, although being slightly more advanced (Fig. 4, middle panels). By October, the abundance was lower (less so at the deepest station at 73.5°N), and the population was strongly dominated by the over-wintering stages CIV (30–40%) and CV (50–70%). The overwintering stages CV and CIV were also dominant at the NCC station in October but with lower total abundances. There were about 20% young copepodites CI-CIII and also some adult females (about 5%, some of them *Calanus helgolandicus*) present in the NCC in October. Some young copepodites and adult females were also present in the Atlantic water stations at this time. A similar situation with dominance of overwintering stages CV and CIV, some young copepodites CI-CIII (about 10%), and a few adult females was also seen at the northernmost station in October (Fig. 4).

The seasonal progression of the copepodite stage index (CSI) summarizes the cohort development of *Calanus finmarchicus* at the four stations (Fig. 5A). The appearance of the first spring generation (G1) is clearly seen as a reduction in the index (to median values of about 3) in April for the NCC station, and in May for the three other stations. The southern Atlantic water station (72°N) showed signs of the new generation in April in some years, reflected in wide interquartile distance and range of CSI values (Fig. 5A). In May, the new generation was developing in Atlantic water with a relative stage distribution resembling that observed at the NCC station one month earlier (Fig. S-1). The situation in June was characterized by considerable variability in CSI, with median index values of 4–5 at the NCC and Atlantic stations. The median CSI decreased between June and August for the NCC station, while it increased for the two northern stations (Fig. 5A). The variability in the stage index was low for the two Atlantic stations in October, with median index values of about 4.5. Similar median values were found at the NCC and the northern stations, although here the variability was somewhat larger. The index values increased during winter to maxima in March or April as the overwintering generation (G0) matured and developed into adults (Fig. 5).

### 3.3. Adult females and males

Mean abundance of adult females was highest in April, May, and June, with values from 1800 to 3200 individuals m$^{-2}$ at the NCC and Atlantic stations (Fig. 6A). Values were lower at the northernmost station with around 500 females m$^{-2}$. Maximum values in the time series were 7600 females m$^{-2}$ in April for the NCC station, and 16,000 m$^{-2}$ in June and 23,000 m$^{-2}$ in October for the southern and northern Atlantic stations, respectively. The abundance of males was highest in March and April with mean values up to 800 individuals m$^{-2}$ at the 73.5°N station (Fig. 6B). The ratio of males to females was relatively high in January, March, and April (0.1–1), and low thereafter (typically 0.05 or less).

The maturation of the population from January to April was reflected in an increased proportion of adult females (Fig. 4B) and an increase in the female/CV index to median values of 0.5 or higher (meaning 75% or more were females) (Fig. 5B). The female/CV index decreased in May and June to median values of −0.75 or lower for the NCC and Atlantic stations. By August, the index had decreased further to uniformly low values with medians typically about −0.95 (meaning that nearly all (>97%) were CVs). Fig. 5B shows the seasonal delay in maturation and reproduction of the *Calanus* population going from south to north as addressed earlier (see Fig. 4). Thus, the maturation of G0 indicated by the female/CV index peaked in March at the NCC station (with many high values also in April) and in April at the two Atlantic stations, while it was still high in May at the northernmost station. The resulting G1 showed lower CSI values (relatively more of the younger stages) going from south to north in May and June (Fig. 5A).

### 3.4. Interannual variability and trends in copepodite abundance and cohort development

The copepodite stage and female/CV indexes showed considerable interannual variability for the late winter to summer sampling periods (March-June), as seen from often large interquartile distances and ranges in Fig. 5. Part of this variability was presumably related to variation in sampling time (Fig. 3). The variability and changes in these indexes provide information on the seasonal progression of generations (overwintering G0, first spring generation G1, second generation G2; see Discussion). The new G1 appeared in April at the NCC station and later in May and June at the Atlantic water and northern stations (Figs. 4 and 5). We therefore examine trends for the April series for the NCC station, and for the June series for the Atlantic water stations (noting that the May series was limited to only six years).

The NCC station showed an increasing trend in abundance of copepodites over the April sampling series which has been taken up to 2016 (Fig. 7). This reflected an increase in the new generation of young copepodites with the youngest stages (CI-II) dominant in the early 2000s and again in the late part of the time series (Fig. 7 and Fig. S-2A). This
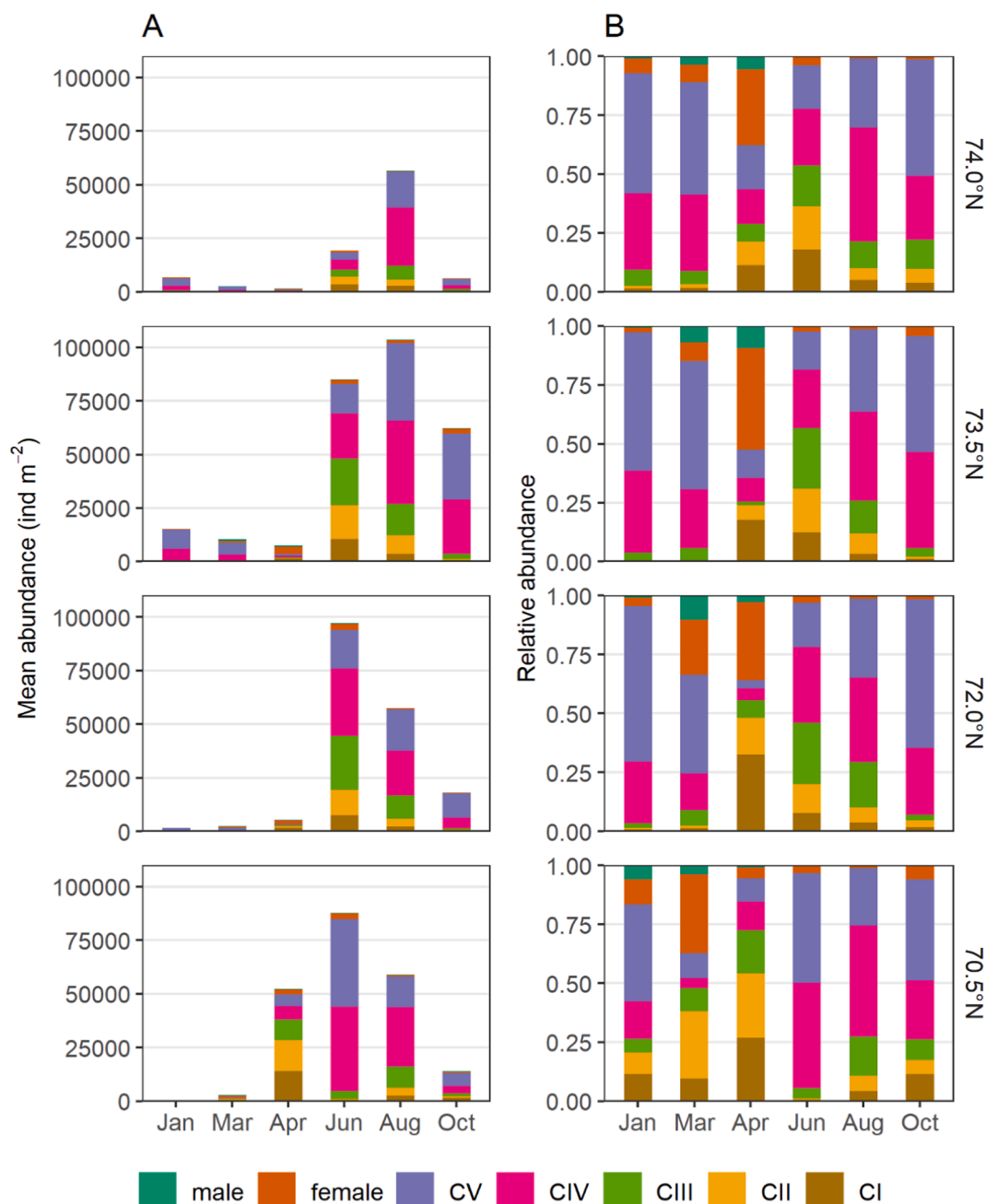
**Fig. 4.** Seasonal patterns of copepodite stage composition of *Calanus finmarchicus* shown as absolute (A) and relative (B) abundances at the four sampling stations on the FB transect. Panels are labelled by station latitude and arranged from south (bottom) to north (top). Values are means over the 1995–2019 sampling period.

pattern was seen in the CSI which showed an overall decline over the time series for the NCC station (Fig. S-2B). The female/CV index showed a general decrease with time (r = −0.85) (Fig. S-2B). The index decreased with increasing abundance of total copepodites (Fig. 8, upper panel). This can be interpreted as a shift from dominance of G0 for the high index values in the early years to G1 associated with the low index values (high abundance of CVs of the new generation relative to females) in the later years of the time series. We note that a shift towards later sampling in April by 2–3 weeks (see Fig. 3) may have caused or contributed to the trends in the April data for the NCC station.

A similar decline of the female/CV index with increasing copepodid abundance was seen in May for the two Atlantic water stations (Fig. 8, middle panel). At this time, the northernmost station (74°N) had low copepodid abundance and high index values, while the southern NCC station had relatively high copepodid abundance and low index values.

The total copepodid abundance at the two Atlantic stations in June varied by two orders of magnitude, from lows around 10,000 individuals m$^{-2}$ to highs of around 500,000 individuals m$^{-2}$ (Fig. 9). The average stage composition showed a dominance of stages CIII, CIV and CV (Figs. 4 and 9, Fig. S-3). 2010 was a year with particularly high abundance at both stations, when young copepodites CI-CIII contributed with more than 300,000 individuals m$^{-2}$. In most years, however, stages CIV and CV dominated (Fig. 9). Apart from the high values in 2010, there was no correlation between copepodite abundance at the two stations over the time series.

The copepodid stage composition showed some fluctuations over the June time series with a positive correlation between the CSI for the two Atlantic stations (r = 0.74) (Fig. 10). The CSI values varied between about 3 and 5 and tended to be lower for the 73.5°N station. The CSI at the 74°N station showed similar fluctuations to the Atlantic water
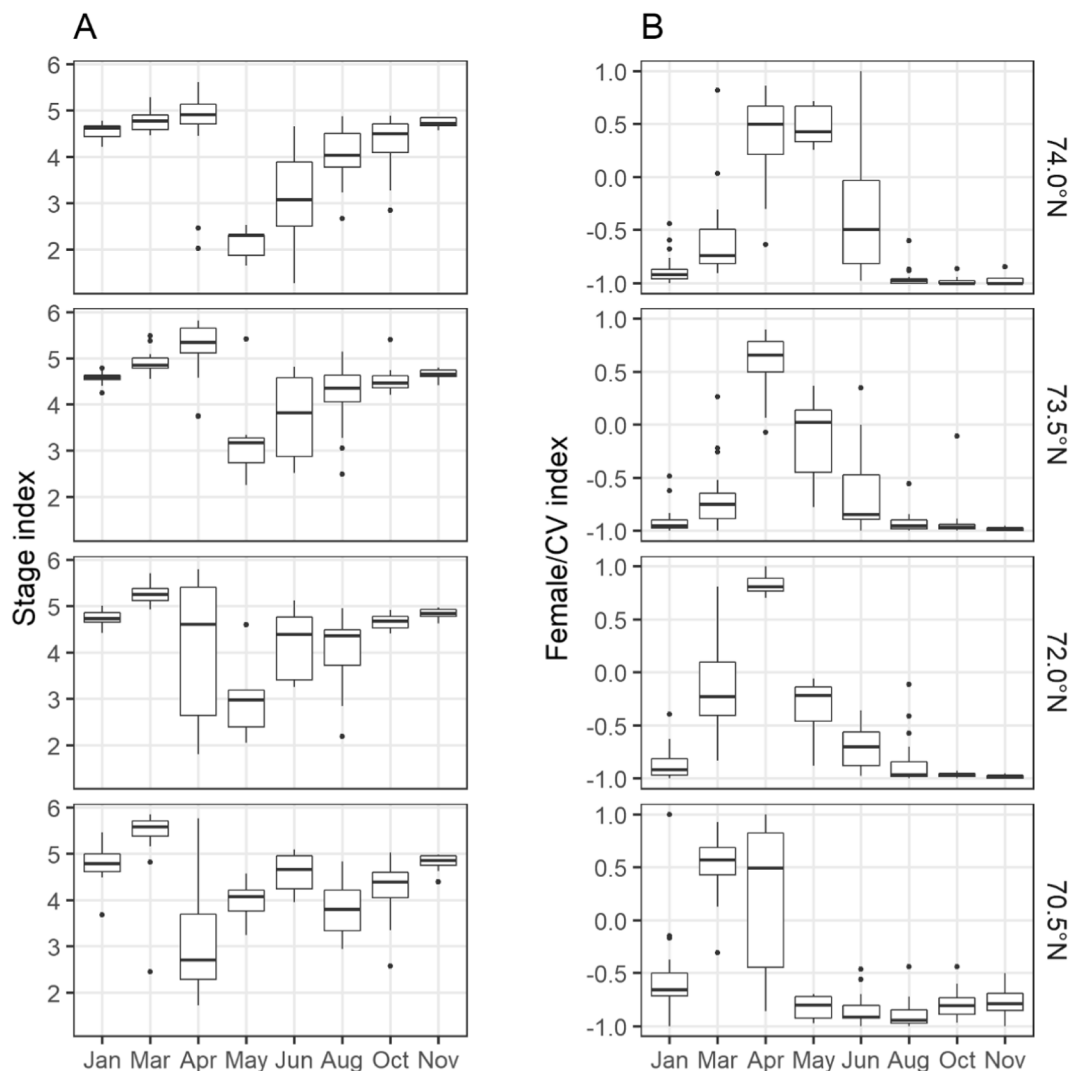
**Fig. 5.** A) Copepodite stage index (abundance-weighted average stage number) and B) adult female/CV index for *Calanus finmarchicus* at the four sampling stations at the FB transect. Panels are labelled (right) by station latitude and arranged from south (bottom) to north (top). Box-whisker plots showing medians (thick horizontal line), interquartile distances delimited by the 25–75% percentiles (box), ranges (5–95%, vertical line), and outliers (dots) for the 1995–2019 data series. The panels show the statistical distribution of the two indexes in each sampling period (month) for the years sampled in each series (see Fig. 3).

stations (r = 0.76 between the 73.5 and 74 stations) and with a pattern of being generally lower than at the 73.5°N station (Fig. 10). We note that the abundance of copepodids at the northern polar front station in June was generally much lower compared to the Atlantic stations (Fig. 4). The tendency of lower CSI values in the late part of the series coincided with earlier sampling in June (see Fig. 3).

The female/CV index in June was low, with mean values of −0.74 and −0.64 for the two Atlantic water stations, reflecting predominance of CVs over females (Fig. 5B). The higher values (reflecting relatively more females) were found for samples with low total copepodid abundance (Fig. 8, lower panel). Compared to the Atlantic water stations, the CSI tended to be higher, and the female/CV index to be lower at the NCC station, while the opposite pattern (lower CSI and higher female/CV index) was seen at the northern station (Fig. 5).

Like in June, the abundance of copepodites of *Calanus finmarchicus* in August varied by two orders of magnitude, from a low of 3000 ind. m$^{-2}$ (72°N station in 1999) to a high of 670,000 ind. m$^{-2}$ (74.0°N station in 2016). The abundance at the Atlantic water stations was < 100,000 individuals m$^{-2}$ for the years between 1998 and 2008, with some higher values in the first few years and from 2010 onwards (Fig. 11). We note that sampling time in August has shifted, from late August/early September in the beginning of the time series towards earlier sampling

after 2010 (Fig. 3).There was a positive correlation for abundance between the August time series for the two Atlantic stations (r = 0.54 for log-transformed data). The total abundance tended to be higher at the 73.5°N station compared to the 72°N station, being about twice as high on average over the time series (Fig. 4A, middle panels). The abundance at the northern station (74°N) was generally lower than for the Atlantic stations in August. The high value in 2016 was exceptional, being five times higher than the second highest value. There was no trend with time in total copepodid abundance at the 74°N station for the August series, and nor for the sample series in June.

The stage composition in August was dominated by the older copepodite stages CIV and CV at all four stations (Figs. 4 and 11). The youngest copepodite stages (CI and CII) generally occurred in low abundances (about 10% on average; Fig. 4B). The CSI for the Atlantic stations varied between 2 and 5 and showed low degree of covariation between the August series for the two stations. The high abundance in Atlantic water in 1995 (73.5°N) was mainly due to young stages (notably CII and CIII), whereas the high abundances after 2007 were due to older stages CIV and CV (Fig. 11).

The female/CV index was generally lower than −0.8 in August for the Atlantic stations (Fig. 5B), reflecting that females represented < 10% compared to copepodite stage CV. The index values were higher in some
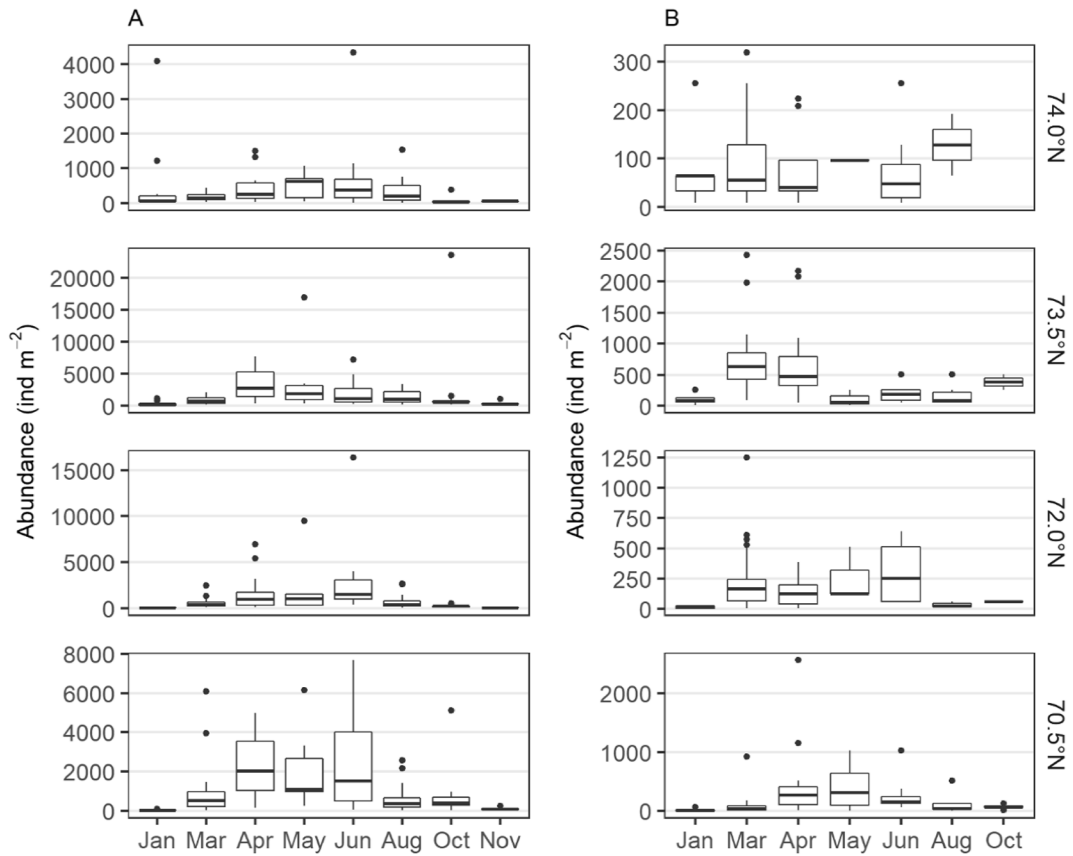
**Fig. 6.** Seasonal patterns of abundances of adult females (A) and adult males (B) at the four sampling stations on the FB transect over the study period, 1995–2019. Box-whisker plots showing medians (thick horizontal line), interquartile distances delimited by the 25–75% percentiles (box), ranges (5–95%, vertical line), and outliers (dots). Note that panels are plotted with different scales on the y-axis.
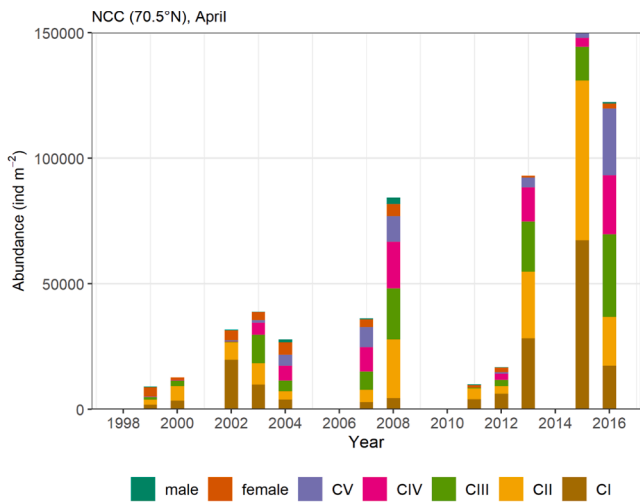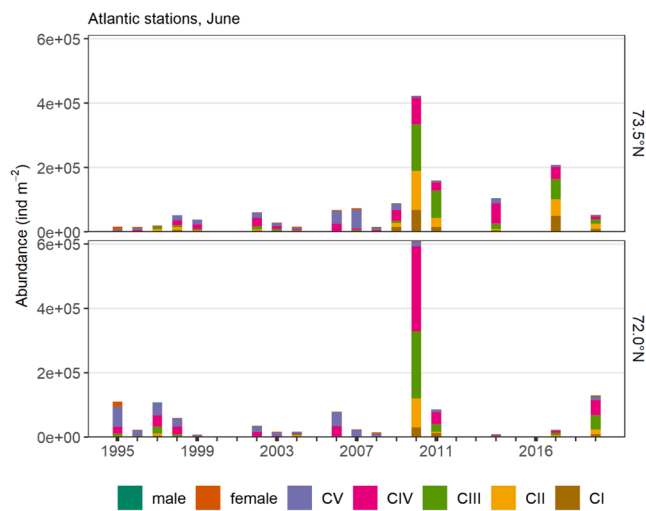


**Fig. 7.** Copepodid stage composition and abundance of *Calanus finmarchicus* at station 70.5°N located in the Norwegian Coastal Current for the April sampling series, 1998–2016. Note that not all years were sampled.

years such as 2000 and 2005 at the 72°N station. These years were characterized by relatively high abundance of younger copepodites (Fig. 11, Fig. S-4). In contrast, a relatively high female/CV index at 73.5°N in 1999 was associated with predominance of older copepodite stages but with very low abundance of total copepodids that year (Fig. 11, Fig. S-4).
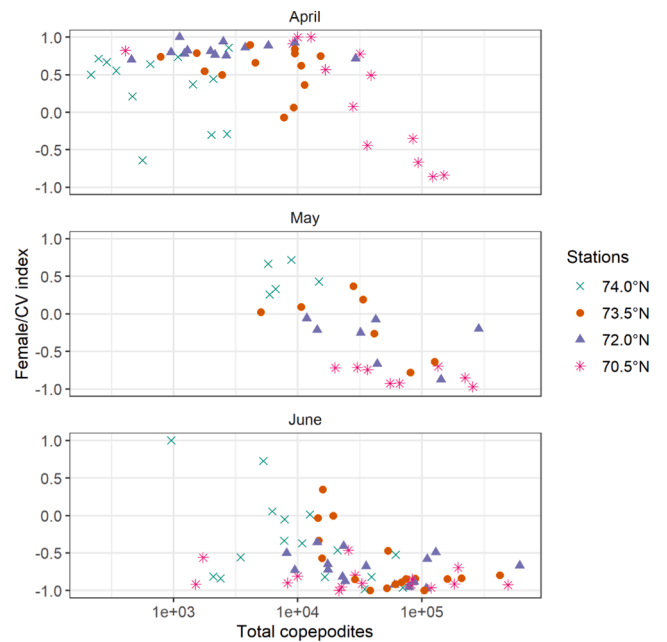


**Fig. 8.** The adult female/CV index plotted against total copepodid abundance for the April, May, and June sampling series for the four stations at the FB transect identified by colored symbols.

**Fig. 9.** Abundance and stage composition of *Calanus finmarchicus* copepodids at the two Atlantic water stations on the FB transect for the June sample series, 1995–2019. Relative (%) stage composition is shown in Fig. S-3.
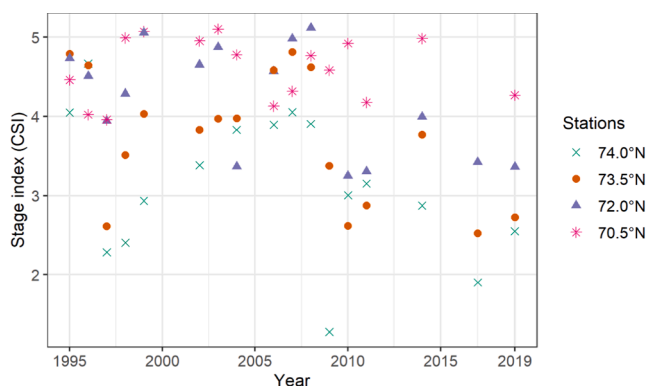


**Fig. 10.** Copepodite stage index (CSI) for the four sampling stations at the FB transect for the June series, 1995–2019. Note that not all years were sampled, and that there is a bias towards earlier sampling in the latter part of the time series (see Fig. 3).
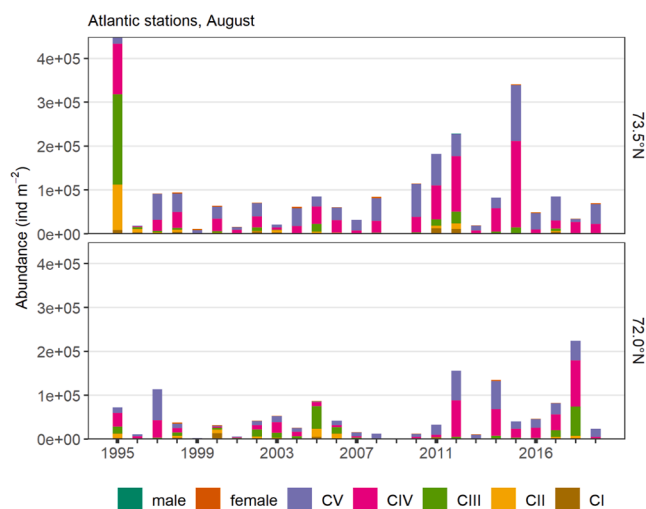


**Fig. 11.** Abundance and stage composition of *Calanus finmarchicus* copepodids at the Atlantic water stations on the FB transect for the August sample series. Relative (%) stage composition is shown in Fig. S-4.

## 3.5. Increase in summer abundance of Calanus finmarchicus copepodids

We have noted the high degree of interannual variability (by two orders of magnitude) for the June and August sampling series, with a tendency of lower abundances (<100,000 copepodites m$^{-2}$) before 2008 or 2009, and higher abundance values (>100,000 m$^{-2}$) for some of the years from 2010 onwards (Figs. 9 and 11). This was most clear for the Atlantic water stations, but also the two other stations displayed some high values in the latter period (data not shown). A GAM model applied to data from the two Atlantic stations showed no significant increase in abundance of CIV-adults with year when analyzing data from the whole seasonal cycle (Table 3). The model demonstrated the pronounced increase from low winter abundances to high summer abundances taking place during the month of May (days 120–150; Fig. 12A), but also the large interannual variability within seasons (points in Fig. 12A). Focusing on data from summer months (June and August) only, our analyses indicated that the abundance of CIV-adults has increased since 2005, though the smoother was only slightly significant (p = 0.033, Table 3) and the annual variability was large (points in Fig. 12B).

## 3.6. Environmental drivers of variability in Calanus finmarchicus development

### 3.6.1. Temperature

Temperature decreased from south to north along the transect, from an average of about 7 °C at the NCC station, to about 2.5 °C at the northern station (Fig. 13). There was pronounced seasonal variation at the NCC station with an amplitude of about 4 °C, from a winter minimum (March) of about 5 °C to a summer maximum (August) of around 9 °C. The southern Atlantic station also showed clear seasonal variation but with lower amplitude to summer maximum of about 6.5–7 °C. For the northern Atlantic station, the seasonal variation was smaller and less regular with seasonal maxima of about 4–5 °C. In contrast to the pattern for the seasonal variation, the interannual variation was larger for the two northern stations compared to the southern stations, with variation between about 1 and 4 °C for the station at 74°N.

Temperature showed increasing trends over the period investigated, again more markedly so for the northern than for the southern stations (Fig. 13, trendlines not shown). This is part of a warming trend since

**Table 3**

Results from GAM analyses assessing the (log$_e$) abundance of *C. finmarchicus* (sum of stages CIV, CV and adults) as smooth functions (s) of day in year and year. Analyses were limited to observations from the two Atlantic water stations (72 and 73.5°N) and run on data both from the whole seasonal cycle and from summer only (June and August). Station was a significant predictor variable only in the model for the whole seasonal cycle, hence this model is given with two intercepts (α). edf: estimated degrees of freedom.

| Whole seasonal cycle: log$_e$(abundance) = α + s$_1$(DayInYear) + s$_2$(Year) + Station | | |
|---|---|---|
| **Family (link)** | gaussian (identity) | |
| **Deviance explained** | 63.2% | |
| **α (Station 72°N)** | 8.60 | |
| **α (Station 73.5°N)** | 9.82 | |
| **n observations** | 250 | |
| **Smoothers** | **edf** | **p-value** |
| DayInYear | 8.55 | $<2 \times 10^{-16}$ |
| Year | 3.33 | 0.109 |

| **Summer:** log$_e$(abundance) = α + s$_1$(DayInYear) + s$_2$(Year) | | |
|---|---|---|
| **Family (link)** | gaussian (identity) | |
| **Deviance explained** | 13.2% | |
| **α** | 10.36 | |
| **n observations** | 81 | |
| **Smoothers** | **edf** | **p-value** |
| DayInYear | 1.00 | 0.608 |
| Year | 2.78 | 0.033 |
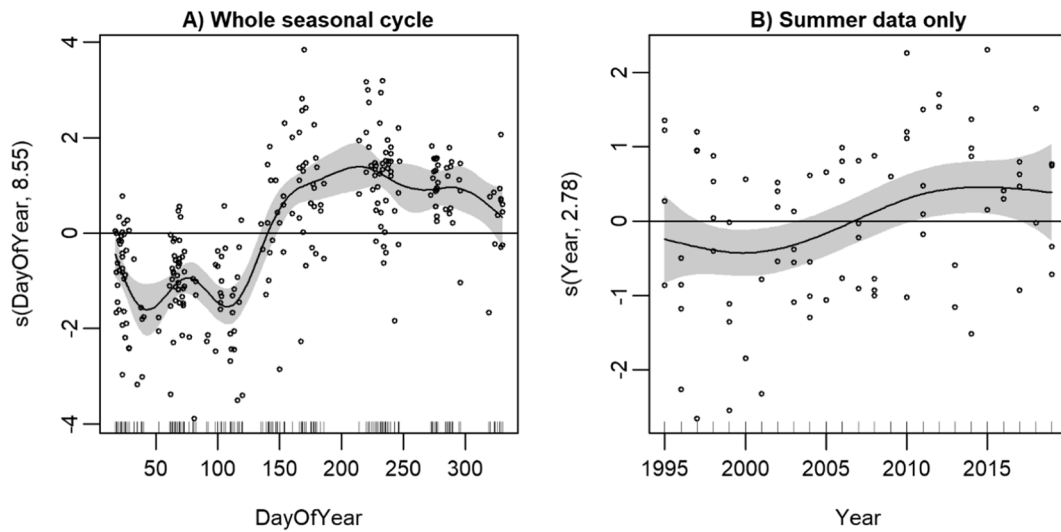
**Fig. 12.** Results from GAM analysis of abundance of *Calanus finmarchicus* ($\log_e$ sum of stages CIV-adult) as a function of day of year and year at the two Atlantic stations. (A) The DayOfYear smoother for data from all sampling occasions. (B) The estimated Year-smoother for observations taken in summer (June and August). The continuous line shows the fitted smoother, with the grey area representing the 95% confidence interval, and the points denote the partial residuals.
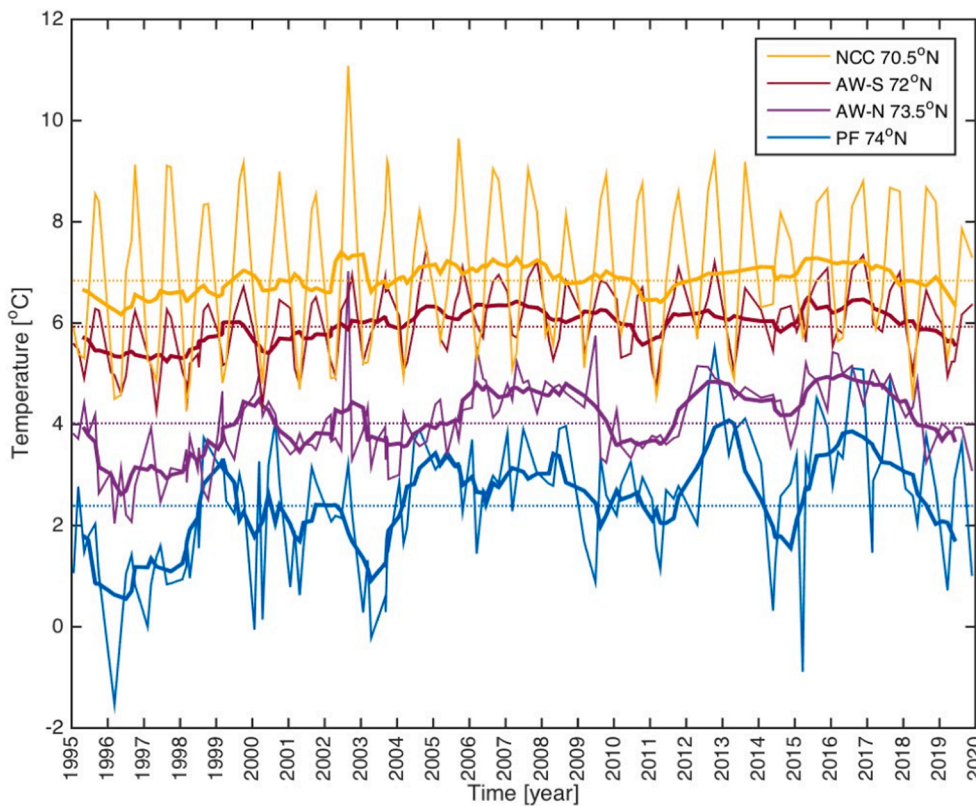


**Fig. 13.** Temporal development of temperature (mean values over the water column) at the four sampling stations at the FB transect from January 1995 to November 2019. The thin lines show the seasonal variation for the sampling periods (see Fig. 3), while the thick lines are smoothed (5-point running average) to remove the seasonal signal. Linear trends of increase in temperature over the series were 0.2, 0.3, 0.5, and 0.7 °C per decade for the four stations from south to north, being statistically significant at the 95% level for the two Atlantic stations and the polar front station but not for the NCC station.

1980, after a cold period in the 1960s and 1970s, and is partly associated with the Atlantic Multidecadal Oscillation (Delworth and Mann, 2000; Polyakov et al., 2003) and partly associated with anthropogenic global warming. The average temperature of the Atlantic water at the FB transect has warmed by nearly 2 °C since 1980, from about 5° to about 6.5 °C in summer (Fig. S-5). There were two waves of warming in the early 1980s and 1990s (Ingvaldsen et al., 2003). Over the time series we consider here (from 1995), the temperature decreased initially in the late 1990s, followed by upswings to local maxima in or around 2000, 2006, 2012, and 2016, with some cooling in the latest years (Fig. 13, Fig.

S-5).

Temperature had a significant effect on the stage composition (CSI) of the developing generation of *Calanus finmarchicus* in June (Fig. 14, Table 4), with a more advanced stage development in the population at higher temperature. This is a combined spatial (stations) and temporal (interannual) effect of temperature. The statistical relationship between temperature and CSI was however not significantly different between the stations (results not shown). Sampling time within the June sampling period also played a role with more advanced stage development (higher CSI) in observations taken later in June. The optimal model for
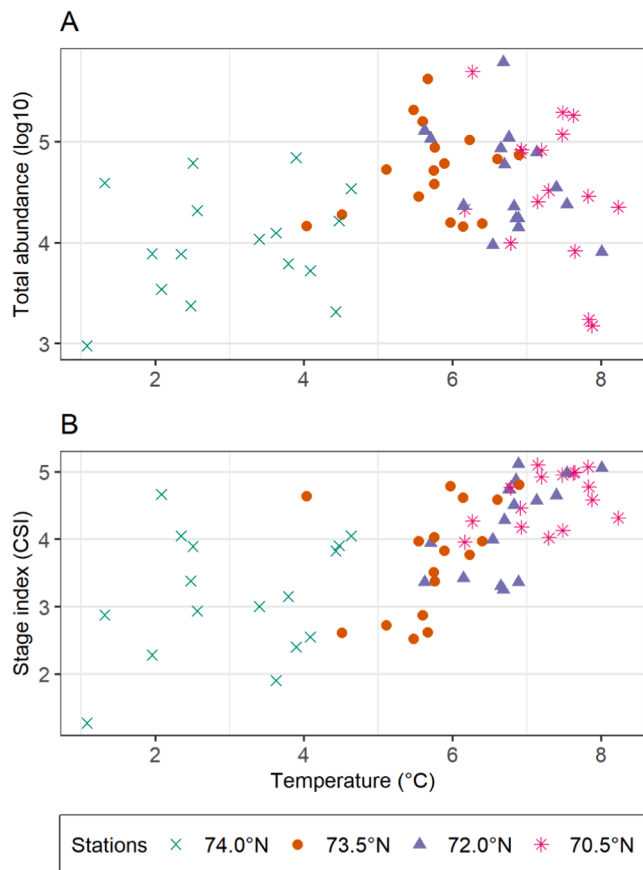
**Fig. 14.** Relationship between temperature in the upper water layer (0–50 m depth) and (A) total copepodite abundance and (B) copepodite stage index for the four stations at the FB transect for the June sampling series, 1995–2019.

**Table 4**

Summary of linear regression model assessing the copepodite stage index (CSI) as a function of mean temperature (°C) in the top 50 m and day of year (DOY) of sampling, using data from the June sampling series for the four stations. Including nitrate concentration (μmol L$^{-1}$) and sampling station (categorical) did not improve the model performance (results not shown). Models were compared using AIC.

| Model | | $R^2$ | df |
|---|---|---|---|
| CSI = $\alpha + \beta_1$(T0-50) + $\beta_2$(DOY) | | 0.53 | 62 |
| **Term** | **Estimate** | **Std error** | **p-value** |
| $\alpha$ (intercept) | −3.57 | 1.44 | 0.016 |
| $\beta_1$ (T0-50) | 0.31 | 0.04 | <0.001 |
| $\beta_2$ (DOY) | 0.03 | 0.008 | <0.001 |

describing the stage composition as a function of the environment included only temperature and day-of-year and captured 53% of the variance in CSI (Table 4). A model of CSI as a function of temperature alone explained 42% of the variance (results not shown).

The total copepodid abundance in June showed a weak relation with temperature for the data from the four sampling stations (Fig. 14A; r = 0.35). The relation was driven largely by lower abundance for the northern station with the lowest temperatures. High abundance values (>100,000 copepodites m$^{-2}$) were found only at temperatures above 5 °C (Fig. 14A).

### 3.6.2. Spring phytoplankton bloom

The winter maximum nitrate concentration in the upper water layer (0–20 m) occurred in March, with lower values (around 7–8 μmol L$^{-1}$) at the NCC station than for the Atlantic and northern stations (11–12 μmol

L$^{-1}$) (Fig. 15). The seasonal decrease of nitrate due to the onset of spring phytoplankton growth started around 1 April and progressed earlier by about a month for the NCC station compared to the others. Thus, 50% of the winter nitrate content was used by mid-April at the NCC station and by mid-May for the Atlantic stations (Fig. 15). The mean chlorophyll $a$ concentration in the upper 20 m was 1 μg L$^{-1}$ at the NCC station in April (maximum 3.6 μg L$^{-1}$; Table S-1). Some early spring growth of phytoplankton had also taken place at the Atlantic stations in April as shown by mean chlorophyll $a$ concentration of 0.8 and 0.3 μg L$^{-1}$ at the two stations, respectively.

There was considerable nitrate left in June at the Atlantic and northern stations (Fig. 15), showing that the spring bloom was still on-going in most years. The seasonal draw-down of nitrate demonstrates that the spring bloom at the FB transect is a prolonged phenomenon, lasting 2–3 months at the NCC station (April-May/June) and around 3–4 months at the Atlantic stations (April-July). This means that the spring cohort of *Calanus finmarchicus* develops in parallel with and within the time frame of the spring bloom. From the scatter of data points (for individual years) around the trend lines it can be inferred that the progress of the spring bloom varied interannually by up to 3–4 weeks, though the interannual variation in sampling time is a confounding factor. We note that the interannual variability tends to exaggerate the apparent duration of the blooms when data from several years are combined compared to the duration in the case of a single year.

The earlier development of the new spring generation of young copepodite stages at the NCC station compared to the Atlantic stations was related to the earlier spring bloom development, reflected in generally higher chlorophyll $a$ content in April. Copepodid abundance at the NCC station in April (Fig. 7) was positively correlated with chlorophyll $a$ (r = 0.49, p = 0.22, n = 8), and negatively correlated with nitrate (r = −0.69, p = 0.03, n = 10). There was a trend of later sampling by about two weeks during the April series (see Fig. 3). The increase in copepodite abundance and the corresponding decrease in nitrate (as a measure of spring bloom development) appear to be mainly a reflection of the successively later sampling during the series (r = 0.80 and −0.89 for copepodid abundance (log) and nitrate, respectively, versus sampling date in April). The results nevertheless suggest a coupling between the new spring generation of *Calanus finmarchicus* and the spring bloom development in the NCC.

### 3.6.3. Advection into the Barents Sea

Due to the advective nature of zooplankton transport into the Barents Sea, we chose two contrasting periods (four 'low *Calanus*' years
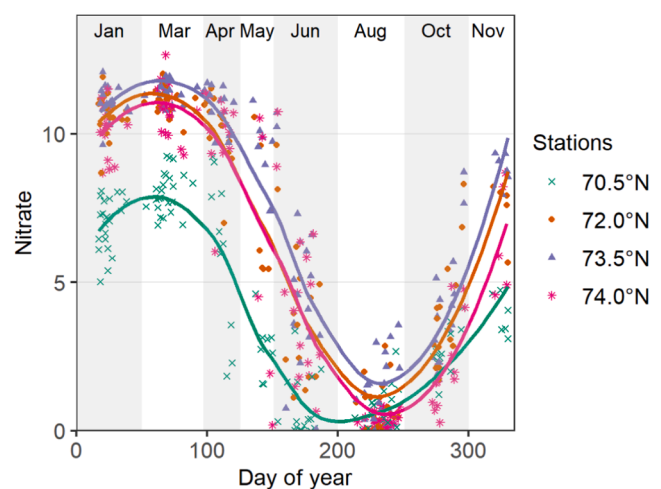


**Fig. 15.** Seasonal changes in nitrate concentration (μmol L$^{-1}$) in the upper mixed surface layer (mean for 0–20 m depth) for the four stations at the FB transect. The data points are for individual years (1995–2019) and the lines are fitted 'loess' smoother curves.

(2001–2004) and four 'high *Calanus*' years (2010–2012, 2014)) for comparison with the physical drivers of water advection variability. The temporal variability in the inflow of both Atlantic Water and Norwegian Coastal Water to the Barents Sea is governed by the atmospheric pressure gradient and the associated local wind stress across the FB transect. Positive (eastward) wind stress favors stronger inflow, while negative (westward) wind stress will tend to reduce the inflow (and in some instances reverse the flow). Calculated wind stress (using the ERA
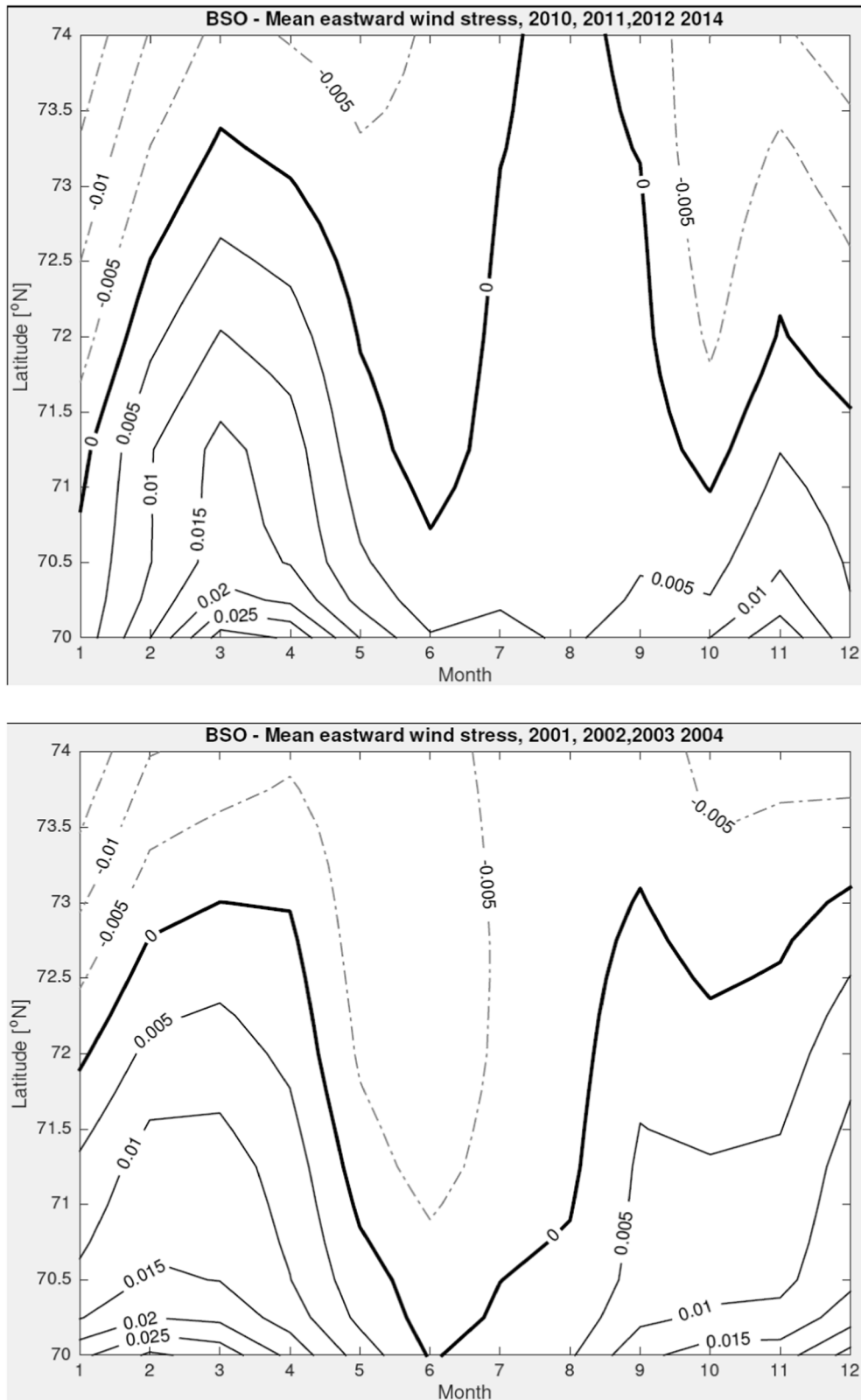


**Fig. 16.** Calculated mean eastward wind stress (positive values; negative values are westward) during the year along a S-N gradient between 70 and 74°N across the western Barents Sea Opening as composites for (A) four 'high *Calanus*' years (2010, 2011, 2012, 2014) and (B) four 'low *Calanus*' years (2001–2004).

Interim atmospheric reanalysis) shows a clear spatial and seasonal pattern across the FB transect, with eastward wind stress in the south and westward wind stress in the north. Moreover, the wind stress is more positive and generally stronger in winter (January-April) and weaker (and partly reversed to westward) in spring and summer (May-August; Fig. 16). The mean situation for the two contrasting periods had weaker eastward and more westward wind stress opposing the inflow in the 'low *Calanus*' years, and more dominating eastward wind stress favoring stronger inflow during the 'high *Calanus*' years (Fig. 16).

Total abundance and stage composition of copepodids (CSI) for the two Atlantic stations in June showed weak correlations with climatic temperature time series (FB and Kola), the winter North Atlantic Oscillation (NAO) index, and modelled transport of water into the Barents Sea across the FB transect (Table S-2). The highest correlation (r = −0.56 for abundance at 73.5°N and modelled Q1 transport) was barely significant at the 5% level (not accounting for multiple comparisons and autocorrelation). The structure of the correlations showed negative values for abundance and positive values for CSI versus NAO and modelled transport in Q1, but these correlations are generally not statistically significant.

## 4. Discussion

### 4.1. Spring development of Calanus finmarchicus delayed from south to north

Our results show a clear pattern of appearance of a spring generation (G1) of *Calanus finmarchicus* which is in general agreement with previous reports for the southwestern region of the Barents Sea (Tande, 1982, 1991; Hassel, 1986; Pedersen et al., 1995; Melle and Skjoldal, 1998; Kvile et al., 2014). One characteristic feature in our data is a delay in timing of appearance of G1 going from south to north along the FB transect (Figs. 4 and 5). Young copepodites of the new generation appeared in April at the NCC station at 70.5°N, while they appeared one month later in May at the Atlantic water stations at 72 and 73.5°N. As seen from Fig. 2, the two Atlantic stations to some degree bracket the Atlantic water domain, being located just to the north of the NCC for the station at 72°N and just south of the Polar Front for the 73.5°N station. There was some influence of the NCC on the southern Atlantic station, shown by occasionally lower surface salinities, which may have contributed to the somewhat earlier cohort development at this station compared to the northern Atlantic station.

The temporal delay from south to north was reflected not only in the appearance of young G1 copepodids but also in the development and maturation of the overwintering generation (G0). This included progressive appearance of males and females and increase of the adult female/CV index, as well as changes of the stage composition overall, including overwintering CIVs and even some CIIIs. At the NCC station, most of the overwintering CVs had developed into the adult stage by March (Fig. 4). The new generation that developed at this station in April was dominated by young copepodids, with stages CI-CIII constituting 40–96% of the total number of copepodids. At *in situ* temperature of about 5 °C (which is about the mean temperature at the NCC station in spring before the onset of the seasonal warming, see Fig. 13), development times are about 3 and 18 days for eggs and nauplii, and 4–5 days for each of the young copepodite stages (Corkett et al., 1986; Campbell et al., 2001). This suggests a duration from spawning to stage CI of about 25 days, and to stage CIII of about 35 days. The cohorts of young copepodites present in April (7–29 April over the years) would therefore have been spawned sometime in March further upstream in the NCC.

The stage composition at the Atlantic water stations in April suggested that the overwintering G0 generation was in an early state of spring reproduction. The females were probably mature or close to maturation, as suggested by the high female to CV index values, and some early spawning had already taken place as evidenced by low abundance of young copepodids (Figs. 4 and 5). By May, the new G1

generation was developing with dominance of stages CI-III at relatively high mean abundances of about 80,000 and 50,000 individuals m$^{-2}$ at the two Atlantic stations. In June, the mean abundance was similar (about 80–90,000 individuals m$^{-2}$) but with a somewhat more advanced stage composition dominated by stages CIII and CIV (Fig. 4). Back-calculating for development rate at 4–6 °C (see Fig. 13) indicates spawning time around late April-mid May (development times of 28–38 days and 34–45 days to reach stages CIII and CIV, respectively).

The spring phytoplankton bloom at the Atlantic water stations was just starting in April, as suggested by low chlorophyll *a* concentration, and nitrate starting to diminish (Fig. 15). The bloom was still progressing in June in most years as shown by remaining nitrate. The back-calculated spawning time in late April-mid May therefore suggests that the peak spawning by G0 took place in the early phase of the spring bloom at the Atlantic water stations. This is in general agreement with what has been reported previously for this area and in similar environments with a prolonged (thermocline-driven) spring phytoplankton bloom in Atlantic water (Melle and Skjoldal, 1998; Niehoff et al., 1999; Hirche et al., 2001). The spring bloom in the NCC progressed earlier, as suggested by earlier nitrate draw-down and more chlorophyll *a* in April compared to the Atlantic water stations. The suggested time of spawning in March for the cohort developing at the NCC station indicates spawning in the early stage of the spring bloom also for the NCC. Early spring bloom in the NCC compared to Atlantic water is related to the stability provided by salinity stratification (Rey, 2004; Bagøien et al., 2012).

The northernmost station was located in the area of the oceanographic Polar Front, and lower temperature is likely to have caused the delayed development here (the effect of temperature is discussed later). The development of G1 at this station was, however, more similar to the northern Atlantic station at 73.5°N than we had expected. The two stations are relatively close (separated by 55 km), and one possible mechanism is that the development of G1 at the 74°N station was dominated by *Calanus finmarchicus* transported with Atlantic water recirculating in the northern end of the FB transect (Skagseth, 2008). Atlantic water is mixed with colder water of Arctic origin in the frontal region, which could explain the similar pattern of variation in stage composition reflected in the CSI (see Fig. 10), as well as the generally lower abundance of *C. finmarchicus* at the frontal station in June (assuming low abundance in the colder water; see Melle and Skjoldal, 1998).

Hassel (1986), Unstad and Tande (1991) and Pedersen et al. (1995) described the appearance of the new G1 generation of *Calanus finmarchicus* in May in Atlantic water in the southwestern Barents Sea. Skjoldal et al. (1987) described results from 6 years of sampling (1979–1984) along a N-S transect in the Hopen Deep area in late spring and early summer (around June). The stage composition of young copepodids suggested an interannual variation of about 3–4 weeks in the estimated timing of maximum copepodid recruitment, related to interannual variation in the timing of the spring bloom (Skjoldal et al., 1987; Rey et al., 1987; Skjoldal and Rey, 1989). Egg production of *C. finmarchicus* was strictly related to the seasonal build-up of chlorophyll *a* by the spring phytoplankton bloom in Atlantic water in the Hopen Deep area (Melle and Skjoldal, 1998). Peak spawning in 1987 was estimated to be around 20 May, which was similar to the back-calculated mean spawning time from copepodid stage composition data for 1979–1984 (Melle, 1998). This is around two weeks later than the estimated spawning time (late April-mid-May) that we inferred from stage composition at the Atlantic water stations in this study. However, it is consistent with the delay we found when going from warmer to colder Atlantic water along the S-N gradient.

### 4.2. Spring invasion of Calanus finmarchicus into the Barents Sea

Our results are in broad agreement with previous studies which have suggested a positive correlation between abundance of the spring

generation G1 of *Calanus finmarchicus* and water transport into the Barents Sea. This was reflected in our study in wind conditions more favorable for water transport in the 'high *Calanus*' years (from 2010) compared to the 'low *Calanus*' years in the early 2000s (Fig. 16). It was also reflected in correlations (although weak and statistically non-significant) between variables reflecting G1 development (abundance and CSI) and modelled water transport, as well as between the G1 variables and the NAO index (Table S-2), where a positive NAO index is associated with larger transport of Atlantic water into the Barents Sea (Ottersen and Stenseth, 2001; Smedsrud et al., 2013; Lien et al., 2017).

Dalpadado et al. (2012) found a statistically significant relationship between variability in zooplankton biomass recorded at FB in August (1997–2010) and measured water flux across the section earlier in spring. Helle and Pennington (1999) used survey data from June-July 1978–1984 to show a positive and significant correlation between average zooplankton biomass in the southwestern Barents Sea and modelled flux of water through the FB transect in June. Zooplankton biomass can be taken as a proxy for *Calanus finmarchicus* biomass since this species dominates the biomass in the southern Barents Sea (Aarflot et al., 2018). Kvile et al. (2017) used the Russian data set (1959–1992) combined with output from a regional 3-D circulation model (Lien et al., 2013a) to illustrate the 'up-stream' spawning location for copepodite stages CI to CIV collected at sampling stations in the southwestern Barents Sea in spring (April-May). They found that copepodites at transects in the Barents Sea Opening area (between about 15–20°E) had largely originated from spawning up-stream in the slope region south to 67–68°N along the Norwegian shelf (see their Figs. 3 and A2). The spring invasion took place with two prongs, one close to the Norwegian coast (NCC branch) and the other between 72 and 74°N (Atlantic water branch). The study also illustrated large interannual variability in the extent of the spring invasion.

Our results do not show as clear relationships between the presence of *Calanus finmarchicus* in the FB region and advection of Atlantic water as some of the previously reported studies do, and they do not reveal the mechanisms involved. A next step could be to examine the interplay between spring development and spring invasion of *Calanus finmarchicus* at the entrance to the Barents Sea, using our 25-year data set on *C. finmarchicus* in combination with remote sensing of sea surface temperature and chlorophyll (Dalpadado et al., 2020) and 3-D modelling of ocean currents, phytoplankton production and development of *C. finmarchicus* (Hjøllo et al., 2012; Skaret et al., 2014).

*4.3. Succession of generations – The issue of a second generation*

Our seasonal data on *Calanus finmarchicus* at the FB transect can at first glance give an impression of one dominant generation per year, which is the G1 spring generation discussed in the foregoing. The mean copepodite stage index was low in April (NCC station) or May, reflecting the high abundance of developing young copepodids of the spring generation G1 (Figs. 4 and 5). This generation developed to a dominance of older copepodite stages CIII-CV in June, with back-calculated peak spawning in late April to mid-May for the Atlantic stations.

However, if we compare the mean copepodid stage composition in June and August they are fairly similar. Young copepodids are still present in August, and the population is on average dominated by stages CIII-CV like in June (see Figs. 4 and 5). Two months is sufficient time to allow a second generation to develop (temperature-dependent development time is about 60 days from egg to adult at 6 °C; Corkett et al., 1986; Campbell et al., 2001). It is unlikely that the copepodites in August represented the same cohort as in June, as this would mean they had had a very slow development. We are sampling in an advective regime, and it seems more likely that the August situation represents a new developing generation of *Calanus finmarchicus*, probably a G2 generation. If this was the case, and the June situation represented the generational transition, it is somewhat surprising that not more CVs were developing into adults. The female/CV index tended to be low in

June (Fig. 5), and it also tended to decrease with increasing total number of copepodids (Fig. 8). This can be interpreted to suggest that most CVs were preparing for overwintering and did not mature into adults and spawn to produce a second generation. However, females were present in June at mean abundance of about 2000 individuals m$^{-2}$, which is similar to the densities of females of the G0 generation which spawned in April-May (Fig. 6). Males were also present in June although with lower abundance than in spring.

The difference between spring and summer is that all surviving CVs developed into adults for the G0 generation, whereas only a small fraction of the CVs of the G1 generation appeared to do so. This might nevertheless provide a sufficiently high number of adult females from G1 to spawn and produce a relatively high number of G2 copepodites, comparable in numbers to the spring (G1) generation. We offer this as a possible explanation for the pattern of copepodite stage composition in our data, particularly from the two Atlantic water stations on the FB transect. An implication of this story would be that the mortality regime would be comparable for the G1 and G2 generations, as judged from roughly similar numbers of spawning females producing roughly similar numbers of copepodids in June and August (Fig. 4).

It is possible that our June sampling (from 2 June to 5 July) failed to capture the main spawning period for the G1 to G2 transition, and that more CVs of the G1 generation developed into adults than we recorded in June. For a mean temperature of the Atlantic water between June and August of 8 °C (Fig. 13), the development time would be about 25–35 days to reach the dominant stages CIII to CV observed in August. This would mean a spawning period in July when back-calculating from the August sampling period (from 31 July to 3 September). Thus, we cannot discount the possibility that the peak spawning by G1 was missed between the June and August sampling periods. The relatively low numbers of young copepodites CI-CII in August (Fig. 4) indicate that the recruitment of G2 copepodids was nearing the end. The relatively high abundance of CIV and CV copepodites at the northern of the two Atlantic water stations (73.5°N) in October suggests, however, a protracted recruitment from late spawning still supplying older copepodids that would contribute to the overwintering generation in the Barents Sea.

Based on data from the Continuous Plankton Recorder (CPR) for 2008–2016, Strand et al. (2020) found a relatively high abundance of young *Calanus* spp. stages in surface-near Atlantic water between northern Norway and Svalbard in late summer and early autumn, and they suggested that these represented a second generation (G2) of *C. finmarchicus*. Skaret et al. (2014) predicted two generations of *Calanus finmarchicus* per season for the inflowing Atlantic water in the southwestern Barents Sea when they ran an individual-based copepod model in a fully coupled, 3D model system with realistic meteorological forcing. This model uses a function for temperature-dependent development modulated by the level of food (modelled phytoplankton) for growth and egg production by the copepods. The model results demonstrate what we have pointed out above, that there is both a potential and likely occurrence of a second generation in the inflowing Atlantic water in summer. In the model, the peak spawning by G1 to produce G2 took place in June, coinciding with our June sampling period. The possibility of a second generation of *C. finmarchicus* in the Atlantic waters of the West-Spitsbergen Current was also reported by Gluchowska et al. (2017).

Our interpretation that only a fraction of CVs belonging to G1 matures into adults to produce a new G2 generation is in line with results for *Calanus finmarchicus* at the Scotian Shelf in Canada obtained by McLaren et al. (1989, 2001). They performed cohort analysis of repeated sampling series over time supported by individual size measurements to demonstrate spatial patterns of generational development. Despite originating from only a fraction of G1, the resulting G2 dominated the overwintering population in some areas (e.g. Emerald Basin in 1990) to become the dominant G0 next spring (McLaren et al., 2001).

The generational succession of *Calanus finmarchicus* at the FB transect must be viewed with due regard to the advective nature of this

inflow area to the Barents Sea. *C. finmarchicus* originates from over-wintering in many places (including the Norwegian Trench in Ska-gerrak, and the Faroe-Shetland Chanel; Heath et al., 2000, 2004), with early spawning in south and progressively later spawning going north (Melle et al., 2014). The two currents, the NCC and the Norwegian Atlantic Current, flow northwards along the Norwegian coast and shelf as relatively narrow structures, with mean current speeds of 10–20 cm s$^{-1}$ (Orvik et al., 2001; Sætre and Aure, 2007). In these current systems, there is scope for two generations (or even three generations in the warmest water of the NCC) developing during spring and summer *en route* to the FB transect. There is likely to be considerable mixing and generational 'smearing' of cohorts originating from spawning in various up-stream locations. In particular, *C. finmarchicus* from the basins of the Norwegian Sea may be advected with Atlantic water onto deeper parts of the shelf (such as around the Halten and Træna Banks on the mid-Norwegian shelf) to populate the NCC (Slagstad and Tande, 1996, 2007; Pedersen et al., 2001; Samuelson et al., 2009; Opdal and Vikebø, 2015).

Our observations of *C. finmarchicus* at fixed stations along the FB transect represent an Eularian dataset obtained from an advective (Lagrangian) environment. We interpret the results to show the passing of a first spring (G1) generation followed by a second G2 generation on their way across the Barents Sea Opening into the southern Barents Sea. The large interannual variability displayed by both the June and August data sets (see Figs. 9 and 11) we suggest reflects the complex nature of the upstream source populations of *C. finmarchicus* and their transports by the currents. Further into the Barents Sea, the copepodids of both G1 and G2 may contribute to the overwintering population of *C. finmarchicus* that makes up the G0 which spawns in cooled Atlantic water in the central Barents Sea next spring (Melle and Skjoldal, 1998; Kvile et al., 2017).

### 4.4. The recent increase in Calanus finmarchicus after 2005 – Is it due to climate change?

Our data suggest that there has been an increase in the summer abundance of *Calanus finmarchicus* in the Atlantic water at the FB tran-sect in the recent years after about 2005. The data is 'noisy' in the sense that there is high interannual variability. A part of this variability re-flects sampling variance stemming from the fact that we have taken only one single net haul sample at each sampling occasion (station and time) (see Skjoldal et al., 2013 and references therein for information on sampling variance). Another reason could be the complex nature of upstream source populations and transports of *C. finmarchicus*, as pointed out in the previous section. Despite the high variability, the data from June and August suggested higher abundance in some of the recent years, particularly from 2010 and later (see Figs. 9 and 11). The GAM model showed a significant effect of year on summer abundance at the two Atlantic stations, with an increasing trend from a minimum in the early 2000s (Fig. 12).

Our results indicate that the increased abundance of *Calanus fin-marchicus* could, at least partly, be explained by wind conditions more favorable for increased inflow in the early 2010s compared with the early 2000s (Fig. 16). However, the volume transport to the Barents Sea does not show any clear long-term trends (e.g. WGIBAR, 2020) and therefore, any increase in *C. finmarchicus* due to advection is likely to be temporary. Another factor impacting the abundance of *Calanus fin-marchicus* being advected to the Barents Sea is the concentration of *C. finmarchicus* upstream in the Norwegian Sea. In the southern Nor-wegian Sea, there has been a decline in *C. finmarchicus* since 2003, apparently related to a climatic shift (Kristiansen et al., 2016, 2019; Dupont et al., 2017). A similar decline in zooplankton biomass (domi-nated by *C. finmarchicus*) around 2003 was also observed in the NCC (61–70°N) in spring (Toresen et al., 2019). Zooplankton biomass (again dominated by *C. finmarchicus*) in the Norwegian Sea (monitored in a comprehensive multi-ship survey in May since 1995) showed a

pronounced decline in the early 2000s to a minimum level in 2006, followed by an increasing trend since 2010 (WGINOR, 2019). These upstream trends in zooplankton biomass and *C. finmarchicus* are partly opposite to what we have found at the FB transect, although the increased biomass in the Norwegian Sea after 2010 may have contrib-uted to the recent increase in abundance of *C. finmarchicus* at the FB transect.

Temperature is a factor linked to climate change that may affect the abundance of *Calanus finmarchicus*. Warming can affect both the timing and rate of development of spring and summer generations of *C. finmarchicus*. Since the spring phytoplankton bloom depends on sta-bility from seasonal warming of the Atlantic water (through thermocline formation), and since early spring growth of phytoplankton determines egg production by spawning female *C. finmarchicus*, early warming could affect the phenology of *C. finmarchicus* with earlier spawning and development of the spring G1 generation. Based on satellite observa-tions of chlorophyll *a* from ocean color, the start of the spring phyto-plankton bloom in the southwestern Barents Sea varied interannually by over a month (from around 10 April to 15 May) for the period 1998–2017 (Dalpadado et al., 2020). This timing is in general agreement with the back-calculated spawning time of late April-early May for *C. finmarchicus*. The satellite data showed a trend (not statistically sig-nificant) towards earlier start of the bloom by about a week over the 20-year time series. Data on *in situ* chlorophyll *a* and nitrate from the FB transect also suggested earlier spring growth of phytoplankton as an average for the years after 2000 (2000–2017) compared to the years before 2000 (1987–1999) (Dalpadado et al., 2020).

Almost 2 °C warming of the Atlantic water since 1980 (Fig. S-5A) was associated with expansion of Atlantic water and a reduction of the extent of Arctic water (Dalpadado et al., 2012). The warming has been char-acterized as on-going 'atlantification' and 'borealization' of the Barents Sea (Dalpadado et al., 2014; Fossheim et al., 2015; Lind et al., 2016; Eriksen et al., 2017; Frainer et al., 2017) and has occurred in 'waves' with alternation between warm and colder years. Since 1995, which marks the beginning of our time series for *Calanus finmarchicus*, the Atlantic water warmed by about 1 °C as a trend (Fig. 13). The interan-nual variation was larger (by up to 3 °C) for the surface water layer at the two Atlantic stations (Fig. 14, Table S-1). We have used the Belehrádek's equation for development time as function of temperature to illustrate the expected effects of temperature on development of the spring G1 generation. For a range of temperatures from 2 to 10 °C, which is about the range experienced by *Calanus finmarchicus* in the Barents Sea (see Figs. 13 and 14), the development time to reach the adult stage (gen-eration time) varies by a factor of 3, from 36 days at 10 °C to 108 days at
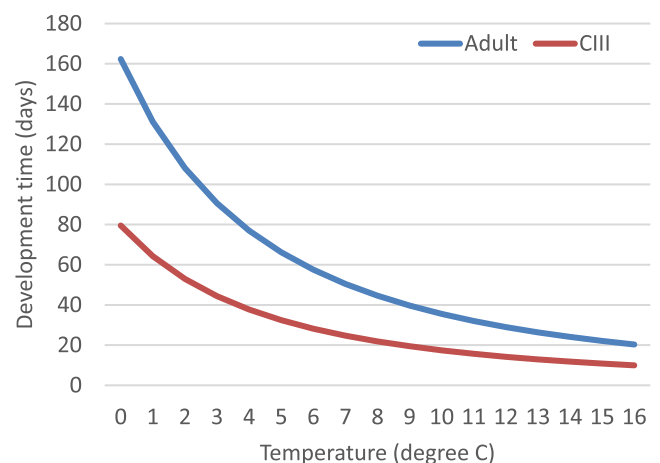


Fig. 17. Development times from egg to copepodite stage CIII and from egg to the adult stage as a function of temperature for *Calanus finmarchicus* using Belehrádek's equation (Bělehrádek, 1935; Corkett et al., 1986) with empirically determined coefficients from Campbell et al. (2001).

2 °C (Fig. 17). The time to reach stage CIII is about half this duration, from about 17 days at 10 °C to 53 days at 2 °C. The dominant copepodite stages at the two Atlantic stations in June were typically CIII and CIV (Figs. 4 and 5) and water temperatures were about 5–8 °C (Fig. 14). A warming of 1 °C represents a forward shift by about 4 days, while interannual variability of 3 °C represents a variation by about 12 days to reach stages CIII-CIV. The positive relationship between copepodite stage index (CSI) and temperature is in general agreement with these indicated changes in development times.

Our results suggest a clear effect of temperature on the seasonal development of *Calanus finmarchicus* at the FB transect (Fig. 14). The early development at the NCC station is driven by an early spring bloom (Fig. 15) but with high temperature contributing to accelerated development of G1 and subsequent G2. The delayed development at the northernmost station is consistent with the lower temperature here compared to the other stations. The nearly 2 °C warming since 1980 may have caused an earlier development of the G1 generation by about 10 days based on the general relationship between development time and temperature. A shift towards earlier spring bloom, as suggested by the results of Dalpadado et al. (2020), may have added even more to this earlier development. Early development of G1 may in turn have influenced the degree to which some G1 individuals have progressed to become mature and produce a second generation (G2) (Fiksen, 2000). It is therefore possible that G2 has become more prominent in the most recent decade compared to earlier.

Kvile et al. (2014) reported effects of temperature on copepodite stage composition of *Calanus finmarchicus* in spring and summer for the Russian time series (1959–1992). The data from spring (April-May) showed a positive relationship between abundance of young copepodids (as well as nauplii) and local (modelled) and regional temperature indices, while the summer data (June-July) showed negative relation between abundance of copepodids and temperature. Since the spring data would reflect the early part of the new G1 generation (front-end of a bell-shaped, normal-like temporal distribution) whereas the summer data would reflect the late part of the spring cohort distribution, the results are consistent with an accelerated development under warmer conditions. Using selected years from the same Russian data set (3 cold and 5 intermediate or warm years), Tande et al. (2000) found large interannual variability with no clear difference between cold and warm years; thus, copepodid abundance was high in both a cold (1979) and a warm (1989) year. They noted that changes between years appeared to be a large-scale phenomenon throughout the study area in the Norwegian and Barents Seas.

The optimum temperature range for the older copepodite stages (CV and adults) based on distribution and abundance data is 6–11 °C (Helaouët and Beaugrand, 2007). The summer temperature of the inflowing Atlantic water at the FB transect is now about 6–7 °C (see Fig. 13 and Fig. S-5A). This is in the lower part of the optimum temperature range for the species. Further into the Barents Sea at the Kola section (at 33.5°E), the temperature of the Atlantic water is about 5 °C as an annual average (Fig. S-5A; WGIBAR, 2020). Based on the temperature conditions, it is expected that the Atlantic water of the southern Barents Sea is becoming a more favorable habitat for *C. finmarchicus*, allowing the species to reproduce successfully further east ('downstream') in the Barents Sea and to increasingly produce a second generation in the Atlantic inflow region of the Barents Sea opening. While a more robust presence and dominance of *C. finmarchicus* is expected under warmer conditions, local wind conditions will likely still play a role in regulating the amount of *C. finmarchicus* transported into the Barents Sea with coastal and Atlantic waters in spring and summer.

## 5. Concluding remarks

The results we report here from 25 years of sampling at the FB transect reveal some clear and consistent patterns but also complexity related to sampling in this advective inflow region to the Barents Sea.

The spring generation (G1) of *Calanus finmarchicus* develops consistently as a well-defined cohort but with a time delay of a month or more going from south to north along the transect. The time delay reflected in the copepodid stage composition is related not only to the rate of development of the new G1 generation but also to the maturation of the overwintering G0 generation. Overwintering CVs undergo maturation with development of gonads, which continues after the molt into adults, progressively during winter (Tande and Hopkins, 1981; Melle and Skjoldal, 1998; Niehoff, 2007). Being ready to spawn at the onset of the spring growth of phytoplankton is an important feature of the life history of *C. finmarchicus* in its core habitat (Melle et al. 2014). The degree to which the adults are ready to mate and spawn by the end of winter has not been much studied. The delay we see in our data when going from south to north (e.g. in the female/CV index) suggests that delayed maturation and readiness to spawn may be a factor influencing successful reproduction of *C. finmarchicus* in the colder Atlantic water in the northern part of its distribution area.

The spring generation G1 occurred in April in the NCC and in May in the Atlantic water. This reflects earlier spring phytoplankton bloom in the NCC due to the inherent stability from salinity stratification as opposed to the delayed spring bloom in Atlantic water which is thermocline-driven associated with the seasonal warming. Back-calculated spawning time from copepodid stage composition in April (NCC) or June (Atlantic water) suggest spawning in March for the NCC and in late April-mid May for the Atlantic water stations. This coincides with the onset of the spring phytoplankton bloom in these two water masses.

Temperature affected the development of the spring cohort G1 consistent with the general effect of temperature on development time. The inflowing Atlantic water has warmed by about 1 °C over the 1995–2019 time series and by nearly 2 °C since 1980. The warming since 1980 is likely to have shifted the G1 development forward by about 10 days due to increased rate of development at higher temperature. In addition, earlier spawning driven by earlier onset of the spring phytoplankton bloom may also have contributed to earlier development of the spring generation. Earlier development may in turn have contributed to an increase in a second summer generation (G2) in the inflow region to the Barents Sea. Earlier and accelerated development is a likely contributing cause for the increased abundance of *Calanus finmarchicus* in the recent decade, resulting from warming associated with climate change. We note, however, that the data is 'noisy' with large interannual variability, which tends to mask the underlying trends based on few sampling stations with infrequent seasonal coverage.

The issue of a second generation of *Calanus finmarchicus* is important in the context of trophic analyses of the Barents Sea ecosystem. This species makes up 70–80% of the total mesozooplankton biomass and drives its variability in the Atlantic water domain in the southern Barents Sea (Aarflot et al., 2018). Our data suggest that the high abundance of copepodids of *C. finmarchicus* in August represent a second generation (G2) spawned in June-July in the inflowing Atlantic water. It appears that only a small fraction of the stage CV of G1 develops into adults, but that the resulting number of spawning females is sufficiently high to produce a G2 of similar magnitude as G1. The arrival of a second generation with the inflowing Atlantic water in summer could be an important feature for the overall productivity and for linkages to plankton-feeding fish such as juvenile herring, capelin, and 0-group fish of several commercial species including Atlantic cod and haddock (Eriksen et al., 2017).

We emphasize the advective nature of the inflow region to the Barents Sea in relation to transport of *Calanus finmarchicus* with the currents and the associated generational succession. Added to this spatial dynamic picture, we also need to consider predation on *Calanus finmarchicus* along the transport routes from the Norwegian Sea towards the Barents Sea. The Norwegian Sea is home to large stocks of three planktivorous fishes: herring, blue whiting, and mackerel (Skjoldal et al., 2004; Utne et al., 2012b; WGINOR, 2016, 2019). Herring,

mackerel and juvenile blue whiting feed to a large extent on *C. finmarchicus*, and with a combined biomass of about 15 million tonnes, they have been estimated to graze a significant fraction of the production of *C. finmarchicus* in the Norwegian Sea (Skjoldal et al., 2004; Langøy et al., 2012; Utne et al., 2012a; Bachiller et al., 2016). The transport of *C. finmarchicus* into the Barents Sea is therefore affected by predation in the adjacent Norwegian Sea ecosystem. The zooplankton biomass in the Norwegian Sea (recorded in May for the upper 200 m) showed a decline by a factor of about 2 in the early 2000s (between about 2002 and 2010) (WGINOR, 2016, 2019). Mesozooplankton is monitored regularly on annual cruises in both the Barents and Norwegian seas using similar methods (WGINOR, 2017, 2016). The coupling between these two ecosystems via transport of *C. finmarchicus* is an item that requires more attention, both through retrospective analyses and in addressing the years to come.

## Author contributions

HRS prepared data and wrote the manuscript. JR analyzed the samples. EB and JMA performed statistical analyses. ØS prepared environmental data. All co-authors contributed to and reviewed the manuscript.

## Declaration of Competing Interest

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.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2021.102574.

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