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Spatial distributions and seasonality of four *Calanus* species in the Northeast Atlantic

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ABSTRACT

This paper analyses spatial and seasonal patterns for near-surface abundances of four *Calanus* species in the Northeast Atlantic based on monthly Continuous Plankton Recorder (CPR) Survey data collected during 2008–2016. *C. finmarchicus*, *C. helgolandicus*, *C. hyperboreus* and *C. glacialis* represent different ecosystems, and water masses with differing oceanographic properties and origins. Hence, these are considered as indicator species in climate change studies. A southern transect between Norway and the United Kingdom represented the northern North Sea, a central transect crossed the Norwegian and Iceland Seas, while a northern transect between Norway and Svalbard crossed the entrance to the Barents Sea. *C. finmarchicus* was prevalent everywhere, while *C. helgolandicus* was mainly confined to the northern North Sea though also documented downstream in the Norwegian Sea as far north as the entrance to the Barents Sea. The ratio of *C. helgolandicus* to *C. finmarchicus* abundances is expected to increase in the northern North Sea and southern Norwegian Sea given continued increases in seawater temperature. *C. hyperboreus* and *C. glacialis* were mainly associated with regions influenced by Arctic waters in the Iceland and Norwegian Seas, and south of Svalbard, respectively. Within Atlantic water masses in the central Norwegian Sea, a distinct second generation of *C. finmarchicus* with surprisingly high late-autumn concentrations of older stages were found. In Coastal water, two or more generations of *C. finmarchicus* occurred, while only one generation was evident in Arctic waters. Young *C. finmarchicus* of the first annual generation showed an earlier timing in Coastal than Atlantic and Arctic waters. The upper range of the temperature niche for both *C. hyperboreus* and *C. glacialis* was found to be around 7 °C. However, the peak occurrence within the study area was in 1–2 °C in Arctic water in the Iceland Sea in April for *C. hyperboreus*, while around 5 °C in Barents Sea Arctic water in July for *C. glacialis*. *C. finmarchicus* was present in all water masses with a peak occurrence in June at around 6 °C. *C. finmarchicus* generally dominated the *Calanus*-biomass, but *C. hyperboreus* in Arctic water in the Iceland and Norwegian Seas in spring, and *C. helgolandicus* in the northern North Sea, could match or exceed the biomass of *C. finmarchicus*.

1. Introduction

The Northeast Atlantic is a highly productive area and home to some of the world's largest commercially harvested fish stocks. In this area characterised by strong seasonal fluctuations in light, the most important herbivore is the group of calanoid copepods belonging to the genus *Calanus*. These enable transfer of vast amounts of energy from seasonally produced phytoplankton to multiannual fish stocks. Due to its ecological importance, the *Calanus* genus has been well studied for many decades (Melle et al., 2014). Several *Calanus* species inhabit the Northeast Atlantic, with their distributional areas partially overlapping. While *C. helgolandicus* is a temperate species common in the North Sea

and as far south as the Mediterranean (Bonnet et al., 2005), the sub-arctic *C. finmarchicus* is a key species in the Norwegian Sea (Østvedt, 1955) and Iceland Sea (Gislason & Silva, 2012). *C. hyperboreus* and *C. glacialis* are arctic species confined mainly to the northern and western parts of the Northeast Atlantic (Jaschnov, 1970; Astthorsson & Gislason, 2003).

In times of climate change, it is important to document species occurrences, so that potential changes in spatial distributions, abundances and seasonality can be detected. A northward shift in the biogeography of calanoid copepods in the eastern North Atlantic Ocean and European shelf seas related to increasing temperature and NAO has been documented based on analyses of multispecies data from the Continuous

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Plankton Recorder (CPR) (Beaugrand et al., 2002). A poleward shift or expansion of habitats in the Northeast Atlantic is clear for *C. finmarchicus* and *C. helgolandicus* (e.g. Bonnet et al., 2005). In the warming northern Barents Sea, the arctic shelf-species *C. glacialis* is under pressure, and it has been speculated that it in the future might become replaced by *C. finmarchicus* (Renaud et al., 2018 and references therein) due to larger areas covered with Atlantic water, diminishing ice coverage and weakened arctic water stratification (Lind et al. 2018).

Until recently, large scale zooplankton data covering the entire range of the Norwegian Sea with a high, monthly sampling frequency throughout the whole year have been lacking. Two new CPR transects, one between Norway and Iceland (crossing the Norwegian and Iceland Seas and covering the Norwegian Basin), and the other between Norway and Svalbard and thereby covering the western entrance to the Barents Sea, were initiated in 2008. The present paper presents the first comprehensive analysis of these new transects, along with a third transect between Norway and Scotland, with a focus on the dominating *Calanus* copepods that inhabit these areas. This paper focuses on basin scale horizontal distributions and seasonality of four *Calanus* species in near-surface waters of the northern North Sea, the Norwegian and Iceland Seas, and the western entrance to the Barents Sea. The species investigated were *C. finmarchicus*, *C. helgolandicus*, *C. glacialis* and *C. hyperboreus*. These are key herbivorous species with distinctly different life history strategies, with different geographical distribution centres, ranging from temperate to arctic ecosystems. However, their habitats overlap both spatially and temporally within the investigated area.

The Northeast Atlantic is characterised by a strong latitudinal gradient in seasonality of solar influx, as well as different water masses characterised by distinct geographical origins, temperatures, salinities and biological communities (e.g. Skjoldal, 2004; Nilsen & Falck, 2006). The Norwegian Sea (Fig. 1) is separated from adjoining seas primarily by topographical features (Skjoldal, 2004), and its upper layers comprise three main water masses; Atlantic water, Arctic water and Coastal water (Blindheim, 2004, Sætre, 2007). Distribution and circulation of water masses is strongly influenced by bottom topography (Blindheim, 2004). The Atlantic water, which is comparatively warm and saline, covers the central parts of the Norwegian Sea. It originates in the southern part of the North Atlantic and flows northward through the Norwegian Sea. Further west, the fresher and colder Arctic water flows southward, separated from the Atlantic water by the Arctic Front (Blindheim, 2004). East of the Atlantic water, the fresher Norwegian Coastal Current flows northward on the shelf along the Norwegian coast (Mork, 1981; Sætre, 2007). The deep Norwegian Basin forms a cyclonic gyre where Atlantic water flows northward along its eastern part. While some of this water flows westward into the Iceland Sea south of Jan Mayen, another component turns southward and continues the cyclonic circulation of the gyre (Blindheim, 2004). The southward flowing water northeast of Iceland mainly consists of cold and relatively fresh water originating from the East Greenland Current (Blindheim, 2004). When meeting the Atlantic water within the Norwegian Sea Gyre, the Arctic front is formed (Blindheim, 2004). Some of the Atlantic water flowing northwards through the Norwegian Sea will continue its northward path on the western side of Svalbard, while another part will turn eastward and flow into the Barents Sea. Fresher Arctic water will flow southward along the eastern side of Svalbard – and some of this will turn clockwise and continue northward along the western coast of Svalbard (Loeng et al., 1997).

The southern part of the study area belongs to the temperate northern North Sea, occupied by Atlantic water masses and hosting the pseudo oceanic temperate species *C. helgolandicus* and the subarctic species *C. finmarchicus* (Wilson et al., 2016 and references therein). A poleward movement of warm water species and a decrease in arctic and subarctic species in this area has been documented (Beaugrand et al., 2002). During recent decades, this area has changed from being considered the southern border for the distribution of *C. finmarchicus* and mainly being occupied by this species, to becoming more dominated by

C. helgolandicus (Reid et al., 2003a,b).

The Norwegian and Iceland Seas, representing the intermediate part of the investigated area, are subarctic and arctic areas occupied by Atlantic and Arctic water masses. The intermediate CPR transect crosses the Norwegian Sea Gyre which is a main distribution centre for *C. finmarchicus* in the North Atlantic (Jaschnov, 1970; Conover, 1988; Sundby, 2000; Heath et al., 2004; Heath et al., 2008). The basins located there allow for overwintering in deep waters, while cyclonic boundary currents help retain the population within the gyres (Halvorsen et al., 2003; Torgersen & Huse, 2005; Melle et al., 2014). *C. finmarchicus* is considered to generally have a one year life cycle in its main distributional area (see Melle et al., 2014 and references therein), but in the warmer southeastern parts and in the Coastal water along Norway this species may produce two or more generations per year (e.g. Wiborg, 1954; Østvedt, 1955; Broms et al., 2009; Bagøien et al., 2012). In neritic areas downstream of the North Sea, even as far north as at the entrance to the Barents Sea, *C. helgolandicus* has also been observed (e.g. Dalpadado et al., 2012; Dupont et al., 2017). Hence, there is some co-occurrence of *C. finmarchicus* and *C. helgolandicus* in the Norwegian Sea, but the level of overlap in space and time is not yet well documented.

C. hyperboreus is an arctic oceanic species and the largest of the *Calanus* species included in this study. *C. hyperboreus* shows adaptations to the cold Arctic and Polar environment with a short feeding season, and it is flexible regarding the duration of its life cycle, which varies geographically. While a one-year life cycle is found in its warmest areas of distribution, two- or multiyear life cycles have been observed in colder regions (Østvedt, 1955; Dawson, 1978; Matthews et al., 1978; Conover & Siferd, 1993; Hirche, 1997; Astthorsson & Gislason, 2003; Broms et al., 2009). West in the Norwegian Sea and in the Iceland Sea, *C. hyperboreus* is associated with Arctic water, where it co-occurs with *C. finmarchicus*. Although *C. finmarchicus* is found in high concentrations in the Arctic water (Astthorsson & Gislason, 2003), it is less adapted to completing its lifecycle there (Broms & Melle, 2007).

The Norwegian and Barents Seas are interconnected as some of the Atlantic water that moves northward along the shelf edge east in the Norwegian Sea, turns eastward into the Barents Sea. The northern part of the investigated area covers this transition zone where *C. finmarchicus* from the Norwegian Sea is brought into the western Barents Sea. Skaret et al. (2014) estimated that around 25% of the *C. finmarchicus* population in the Barents Sea is advected into the area from the Norwegian Sea. *C. finmarchicus* in the Barents Sea is mainly associated with the Atlantic water, while the Arctic water in the northern part of the Barents Sea is dominated by the arctic species *C. glacialis*. *C. glacialis* is generally considered to be an arctic shelf species with a 1–2 year life-cycle (Tande et al., 1985; Conover, 1988; Melle & Skjoldal, 1998; Broms et al., 2009), and is the dominating *Calanus* species in terms of biomass in the eastern and northern parts of the Barents Sea (Aarflot et al., 2018). The length of the life cycles depends on environmental conditions (Tande et al., 1985; Melle & Skjoldal, 1998), and thus enables utilisation of the short annual spring bloom in the arctic as well as coping with prolonged ice cover (Slagstad & Tande, 1990). The outflow of Arctic water from the Barents Sea follows the southern coast of the Svalbard archipelago until it meets the West Spitsbergen Current and turns north along the western coast of Svalbard (Fig. 1) and is thus the area covered by the northern CPR transect.

The present study analyses spatial distributions and seasonality of the four species in the *Calanus* complex in the Northeast Atlantic. Emphasis is on comparing seasonality in water masses with different origins and characteristics, as well as spatial distributions along north–south and east–west gradients. In addition, numerically dominant copepod taxa are presented for each area and season for comparison with the abundances of *Calanus* spp. Finally, we explore the thermal niches of the four species, and show how water masses play an important role in interpreting these. We believe that these results might prove important when predicting future ecosystem dynamics in a

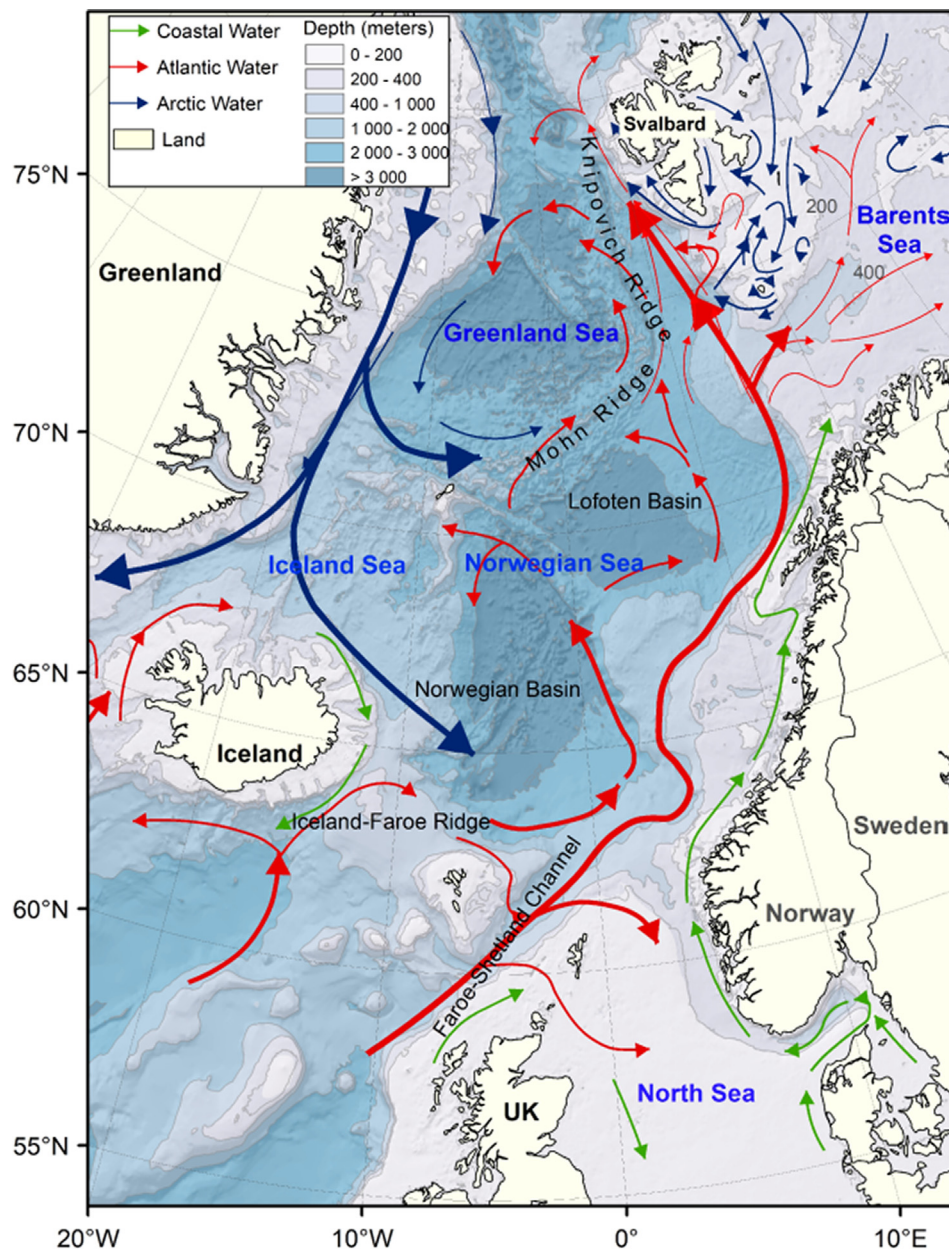


Fig. 1. Map of the Nordic seas, the northern North Sea and the western Barents Sea with topography and main upper currents. Red arrows show currents with Atlantic water, blue arrows show currents with Arctic water, and green arrows show Coastal currents.

warming world.

2. Materials and methods

2.1. The Continuous Plankton Recorder

The CPR (Batten et al., 2003; Reid et al., 2003a,b; Richardson et al., 2004, 2006) was used to collect zooplankton community data from near-surface waters. In summary, the CPR is towed using ships of opportunity such as merchant ships and ferries at a standard depth of approximately 7 m (Richardson et al., 2006). Seawater enters a small, square opening of 1.61 cm² in the front end of the device, and flows through an internal and expanding tunnel, before leaving through its rear end. As the seawater flows through the system, its associated plankton is caught on a 270 µm silk mesh and covered by another layer of silk. The resulting double layer of silk, with the plankton caught in between, is wound around a spool in a formalin tank so that the

plankton is preserved for subsequent taxonomic analysis. After the survey, the different parts along the silk, and the plankton collected there, are related to geographical position during the sampling. See Richardson et al. (2006) and references therein for detailed descriptions of the sampling method and how the collected plankton are processed in the laboratory after the survey. The CPR dataset gives the counts of individuals per taxon per sample which represents a horizontal tow of about 18,520 m or 10 nautical miles. With a mouth opening area of 1.61 cm², the filtered volume of seawater is equivalent to about 3 m³ per sample. Note that the counts are not given on a true continuous scale, as these during the laboratory processing are allocated to pre-specified count-classes, and therefore rather should be considered as semi quantitative (Colebrook, 1979; Batten et al., 2003; Richardson et al., 2006).

CPR data from three transects covering the years 2008–2016 were analysed in the present study (Fig. 2). The dataset comprises the whole seasonal cycle with a monthly resolution, spans the latitudinal range

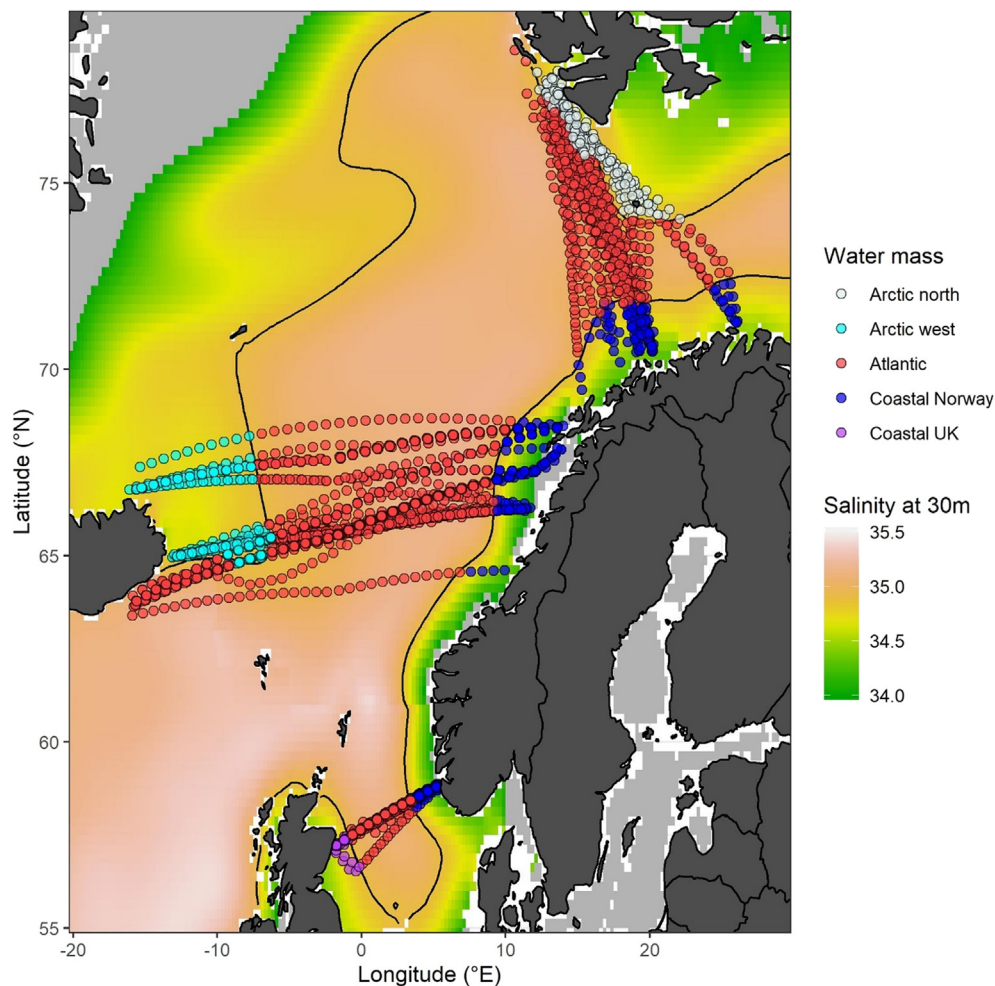


Fig. 2. Assignment of water mass to the CPR data. Each CPR sample is shown as a dot with colour indicating classification to water mass. Salinity is based on annual climatological data at 30 m depth from WOA18 in the period 2005–2017. White areas are WOA18 missing data and light grey areas are water with salinity less than 34. The contour line is set at salinity = 34.9.

from around 57 to 78°N, and includes both coastal and oceanic regions. In this paper, we use the following terms; the “southern transect” runs between Stavanger (Norway) and Aberdeen (Scotland), the “central transect” goes between the Norwegian west coast (about 67°N) and Iceland, while the “northern transect” is between the northern Norwegian Coast and Longyearbyen (Spitsbergen). The three transects cross different ocean areas, including the northern North Sea, the Norwegian Sea, the Iceland Sea, and the western entrance to the Barents Sea. Results from the central and northern transect are previously unpublished while the southern transect has been in operation for a long time and is included in several published CPR studies. The rationale for including the 2008–2016 period of the southern transect in this study was to; (1) increase the north–south gradient of the study area in relation to *Calanus* sp. phenology and abundance, and also to provide an established latitudinal point of reference for comparison, (2) cover the whole core and fringe area of *C. finmarchicus* in the Nordic Seas, (3) study how *C. helgolandicus* is transported northwards along the Norwegian coast and crosses the more northerly transects and (4) use the southern transect as baseline of earlier CPR investigations for comparison with our study. A total of 4082 CPR samples are included in the analysed dataset. CPR data south of 70°N are available online (CPR Survey Data Catalogue) as monthly gridded means (1x1°) of abundance and sampling effort for a large number of species and taxa.

The groups of developmental stages for the *Calanus* species are addressed the following way in this paper. For all *Calanus* species, the reference to older stages comprises stages CV–CVI, while the reference

to younger stages of *Calanus* spp. includes stages CI–CIV of all *Calanus* species except *C. hyperboreus*. Note that Richardson et al. (2006) commented that older stages of *C. hyperboreus* in some cases probably include individuals of stages CIII and CIV.

2.2. Environmental data

2.2.1. Water masses

Samples with salinity above 34.9 at depth of 30 m were classified as “Atlantic” water, while samples with lower salinities along the Norwegian and UK coasts were classified as “Coastal Norway” and “Coastal UK”, respectively. The remaining samples with salinity less than 34.9 at depth of 30 m were classified as either “Arctic west” if in the vicinity of the Iceland Sea or as “Arctic north” when in or near the Barents Sea (Fig. 2). We refer to Blindheim (2004), Sætre (2007) and Ingvaldsen et al. (2009), and references therein, for a description of the main water masses, and their properties and classification in the study-area.

2.2.2. Temperature and salinity

Relating the numerical observations of zooplankton species and groups to key environmental parameters, data from the NOAA World Ocean Atlas 2018 (WOA18) were used. The recorded longitude, latitude and date of each CPR sample were used to extract the correct temperature from WOA18 monthly averaged climatological data on a 1/4° grid from the 2005–2017 period (Locarnini et al., 2018). This period

covers the whole CPR data series presented in this paper. The temperature assigned each CPR sample was extracted from 30 m depth. In one instance, temperature from depth of 10 m was used due to insufficient bottom depth at the recorded CPR station. Values for salinity (Zweng et al., 2018) were extracted from WOA18 and linked to the CPR data in the same way as for temperature, but here using the WOA18 annual salinity climatological data instead of monthly averages (see Fig. 2).

2.2.3. Calculations of *Calanus* sp. biomass from abundance

The *Calanus* species included in this paper vary in body size. Since the CPR data report numeric abundance of species, or species stage groups, we estimated biomass for the different species on basis of the allometric relationships between individual body mass and average prosome length as suggested by Richardson et al. (2006). The allometric relationship used is $W = 0.08 * L^{2.1}$ (Peters, 1983), where W is calculated individual wet weight (mg) and L is prosome length (mm). Average prosome lengths of adult females for the four *Calanus* species used in the calculations are from McLaren et al. (1988) and references therein and set at *C. finmarchicus* = 2.84 mm, *C. helgolandicus* = 2.72 mm, *C. glacialis* = 3.55 mm and *C. hyperboreus* = 6.80 mm. Note that we thereby indirectly assume that all individuals in the CV-adult groups are of the same size as adult females.

2.2.4. Numerically dominant copepods

To compare the abundances of *Calanus* spp. with other common copepod species registered in the CPR data, a list of frequently occurring species was made. The mean occurrence of all copepod species or taxa in our CPR dataset was first calculated and arranged in decreasing order. From this list, all groups representing larger species or taxa, for instance *Paraeuchaeta*, were excluded. Further, groups that include the sum of several different taxa (e.g. Copepods total, Para-Pseudocalanus) were omitted. Unidentified species of a given genus (e.g. “*Centropages* spp. Unidentified”) were omitted when identified species of the same genus were available (e.g. *Centropages typicus*). Finally, one group at the Order level (Harpacticoida) was removed. From the list of remaining taxa, representing the most numerous species or groups of copepods, the 20 most numerous were selected for further analysis.

2.3. Data preparation and analysis

All data preparation and analysis was performed using the software environment “R” (R Core Team, 2018) and the library “Tidyverse” (Wickham et al., 2019). The number of samples collected along each transect per month and water mass, combining all years, is shown in Fig. 3. Note that no data exist from January and February on the northern transect. Data for all years (2008–2016) were combined, and

samples collected both during day and night were included. The average count of individuals per zooplankton taxon per sample was calculated for all combinations of transect, water mass and month. The heatmap in Fig. 4 represents grids of 1.5 decimal degrees in the north-south or east-west directions. For the spatiotemporal maps (Figs. 5–9), data points along each transect were grouped according to the ICES statistical rectangles (0.5° latitude \times 1.0° longitude, ICES, 1977), and the mean count of individuals for each zooplankton taxon was calculated for all combinations of ICES rectangle and month.

3. Results

3.1. Spatial distributions and seasonality of *Calanus* spp.

The older stages of *C. finmarchicus* were observed along the entire range of all three transects, covering both coastal and oceanic areas (Figs. 4 and 5). This reflects that the habitat of this species comprises the North Sea, the Norwegian Sea, the Iceland Sea, as well as the entrance to the Barents Sea, and that it inhabits areas covered by all the main upper water masses in the study area (Coastal water, Atlantic water and Arctic water). *C. finmarchicus* displayed a marked seasonality that differed geographically (Figs. 4 and 5). In January, *C. finmarchicus* was practically absent everywhere in the available data. In February, the older stages appeared in low numbers along the whole central transect, and in the eastern part of the southern transect. During March and April, the numbers continued to rise along all transects. On the central and northern transects, the increases seemed to be strongest in the deep, oceanic regions while on the southern transect the increase was highest in the eastern part. In May, the numbers declined in the mid regions of the central and northern transects, but increased in the coastal areas of Norway, Iceland and Svalbard. In June, the numbers increased again in the oceanic parts of the central and northern regions, while the level was low near the coast of Iceland. From July to September, the levels declined along the northern transect, with the effect being most evident near the coasts of Norway and Svalbard. Along the central transect during the same period, the numbers decreased in the eastern part, though remaining rather high in the western part even as late as September. Clear decreases were seen near the coasts of both Norway and Iceland. On the southern section, the numbers had now decreased to low or moderate levels. In October, the levels were still high on the central transect and especially in the mid region, and a marked drop was evident over the whole northern transect. In November and December, the abundances were generally decreasing to low or very low levels in most regions, although somewhat elevated numbers remained near the coasts of Iceland and Svalbard (Figs. 4 and 5).

The older stages of *C. helgolandicus* were mainly confined to the

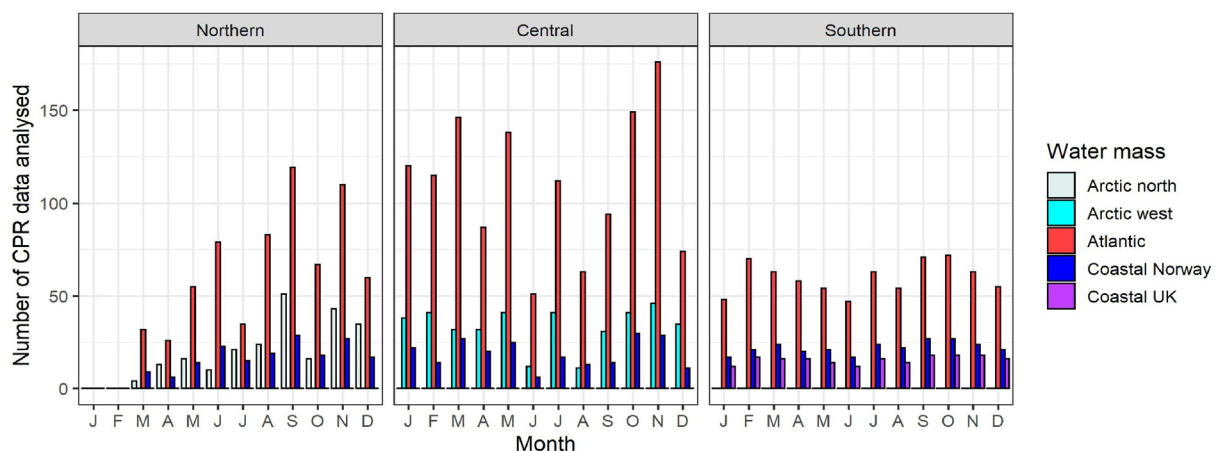


Fig. 3. The number of samples for each month along the southern, central and northern transects and the respective water masses for all years combined.

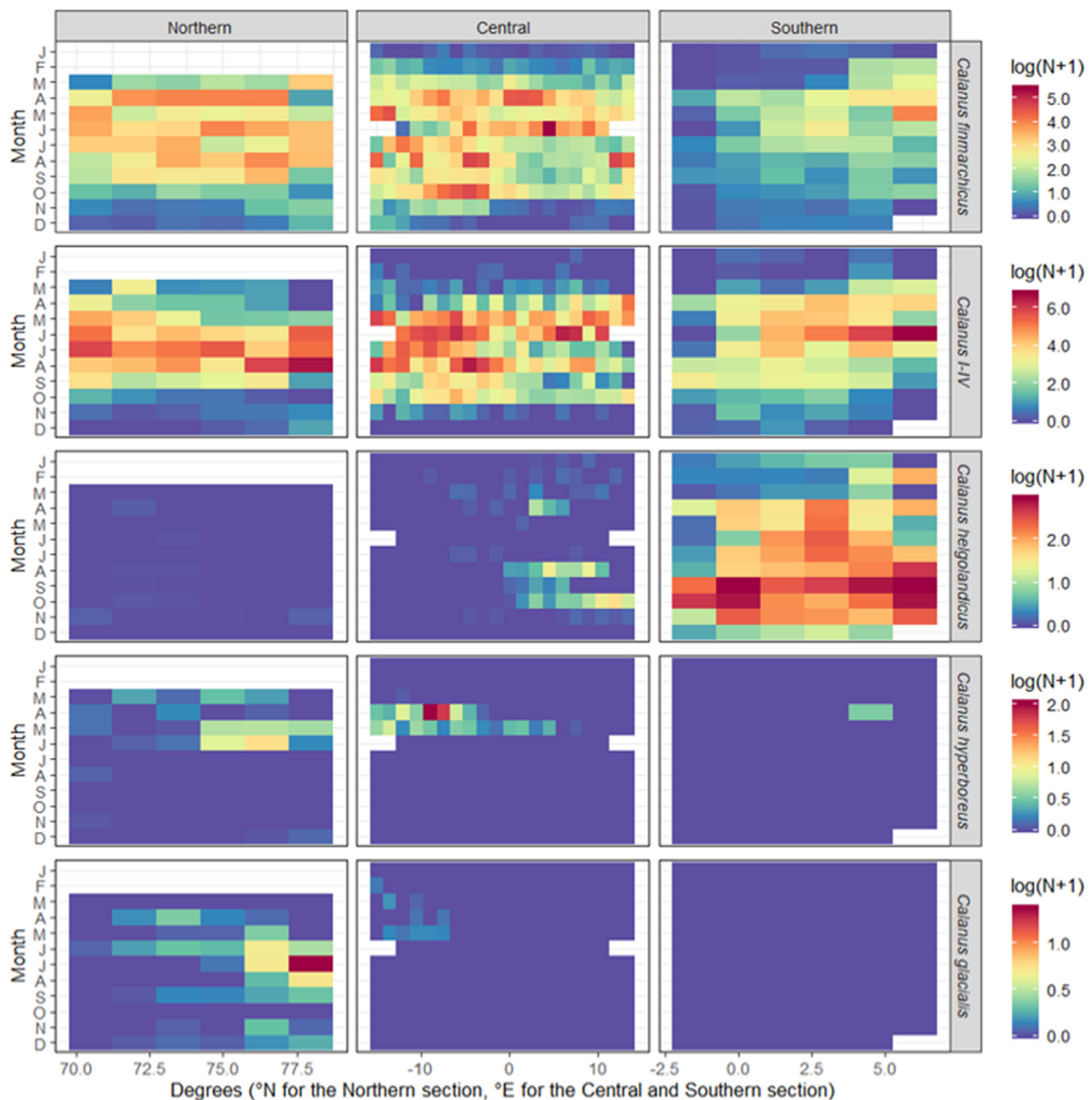


Fig. 4. Monthly abundances (log_e-scale) of *Calanus* species along the three transects. The abundance represents the average count per sample, corresponding to ca. 3 m³.

southern transect, where its numbers were highest, but at times it was also relatively abundant along the eastern part of the central transect (Figs. 4 and 7). Despite occasionally being recorded along the northern transect, the abundance there was always low. On the southern transect, *C. helgolandicus* was present throughout the year. Abundances were rather low from January to March. In April, the numbers in the south increased markedly, and stayed high until November. Numbers were higher in the eastern than the western part from January till about August, after which the levels were higher in the western part of the transect (Fig. 7).

Along the central transect, low numbers of *C. helgolandicus* were recorded most of the year, even in the middle of the oceanic region, and some relatively high values occurred in April offshore on the Norwegian side. However, these high April observations all occurred within an interval of only a few hours, and hence represent one occasion rather than a general pattern. Apart from that, rather high abundances were registered both near shore and further into the oceanic region on the Norwegian side of the central transect from August to October. Still, the

numbers there were not as high as on the southern transect (Figs. 4 and 7).

The older stages of *C. hyperboreus* (but possibly including some CIII-CIV) were almost exclusively seen along the central and northern transects, but we note that the species was recorded on the eastern part of the southern transect in April (Figs. 4 and 8). Along the northern transect, abundances increased in March and April and peaked in May and June, while along the central transect the abundances peaked in April and May and were negligible during the rest of the year. Towards Iceland along the central transect, abundances of *C. hyperboreus* were higher on the more northerly than southerly located stations (Fig. 8). This reflects that *C. hyperboreus* in that area were generally more common at stations classified to represent Arctic than Atlantic waters, as indicated by the salinity isoline in Fig. 8. *C. hyperboreus* numbers were markedly highest in the northern part of the northern transect, and in the western part of the central transect (Figs. 4 and 8), which is where these two transects are most strongly influenced by cold, Arctic waters.

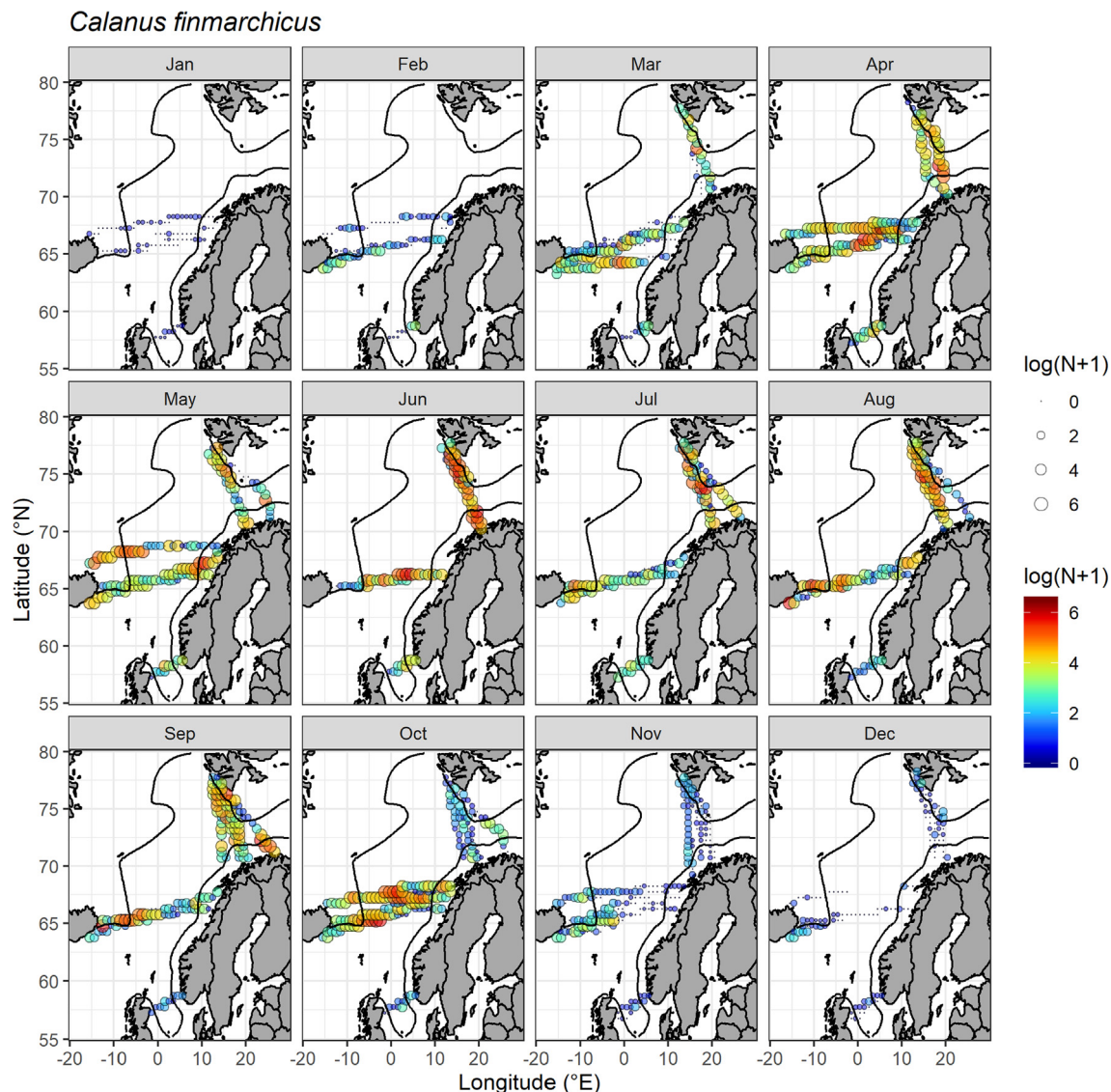


Fig. 5. Monthly abundances (log_e-scale) of *Calanus finmarchicus* (CV-CVI) per spatial grid cell along the three transects. The abundance represents the average count per sample, corresponding to ca. 3 m³. The contour line is set at salinity = 34.9.

The older stages of *C. glacialis* mainly occurred along the northern transect, with abundances increasing with latitude towards Svalbard (Figs. 4 and 9). Its numbers there were highest in June, July and August, but the species was recorded in the area most of the year. Low numbers of *C. glacialis* were also recorded in the western part of the central transect off Iceland during late winter and spring, but there only at the northernmost stations that were classified as representing Arctic water (Fig. 9).

The younger stages of *Calanus* spp. (all species except *C. hyperboreus*) were observed across the entire range of all three sections (Figs. 4 and 6). The seasonality was strong, and differed within the study area. On the southern transect, young stages were observed most of the year, increasing from low levels in January to rather high levels by April. The numbers remained high during May and June, thereafter dropped to a somewhat lower but still significant level that lasted until October, and decreased further to a low level in December (Figs. 4 and 6). Along the central transect, only a few individuals were observed in January, but in February there was a notable increase. During March and April, the levels increased markedly along the transect, although in April the concentration was much higher near the Norwegian coast and somewhat lower near the coast of Iceland than elsewhere. In May and June, the numbers were high all along the transect. In July, the

numbers were lower along the eastern part of the transect than in June, but in August they were rather high again over the whole transect. From September, the levels decreased all along the transect until December when young stages were practically absent. Along the northern transect, data are lacking for January and February. In March, presence of young stages was evident along most of the transect, with the numbers increasing through April and May, and particularly so in the southern part of the transect. Abundances were high across the whole northern transect in June, increasing further in July and August. The numbers decreased in September, and generally reached minimum levels from October to December (Figs. 4 and 6).

There was both spatial and temporal overlap between *Calanus* species in the investigated area. In the northern North Sea, *C. helgolandicus* and *C. finmarchicus* co-occurred, especially during the period April to July. These two species also co-occurred in the eastern part of the Norwegian Sea, which is downstream of the North Sea, but there mainly in autumn. In and towards arctic areas, the three species *C. finmarchicus*, *C. hyperboreus* and *C. glacialis* co-occurred. In western part of the Norwegian Sea and in the Iceland Sea, *C. finmarchicus* and *C. hyperboreus* existed together in upper water masses in April and May, while *C. glacialis* was seen only occasionally. At the entrance to the Barents Sea, *C. finmarchicus* and *C. hyperboreus* co-occurred in March,

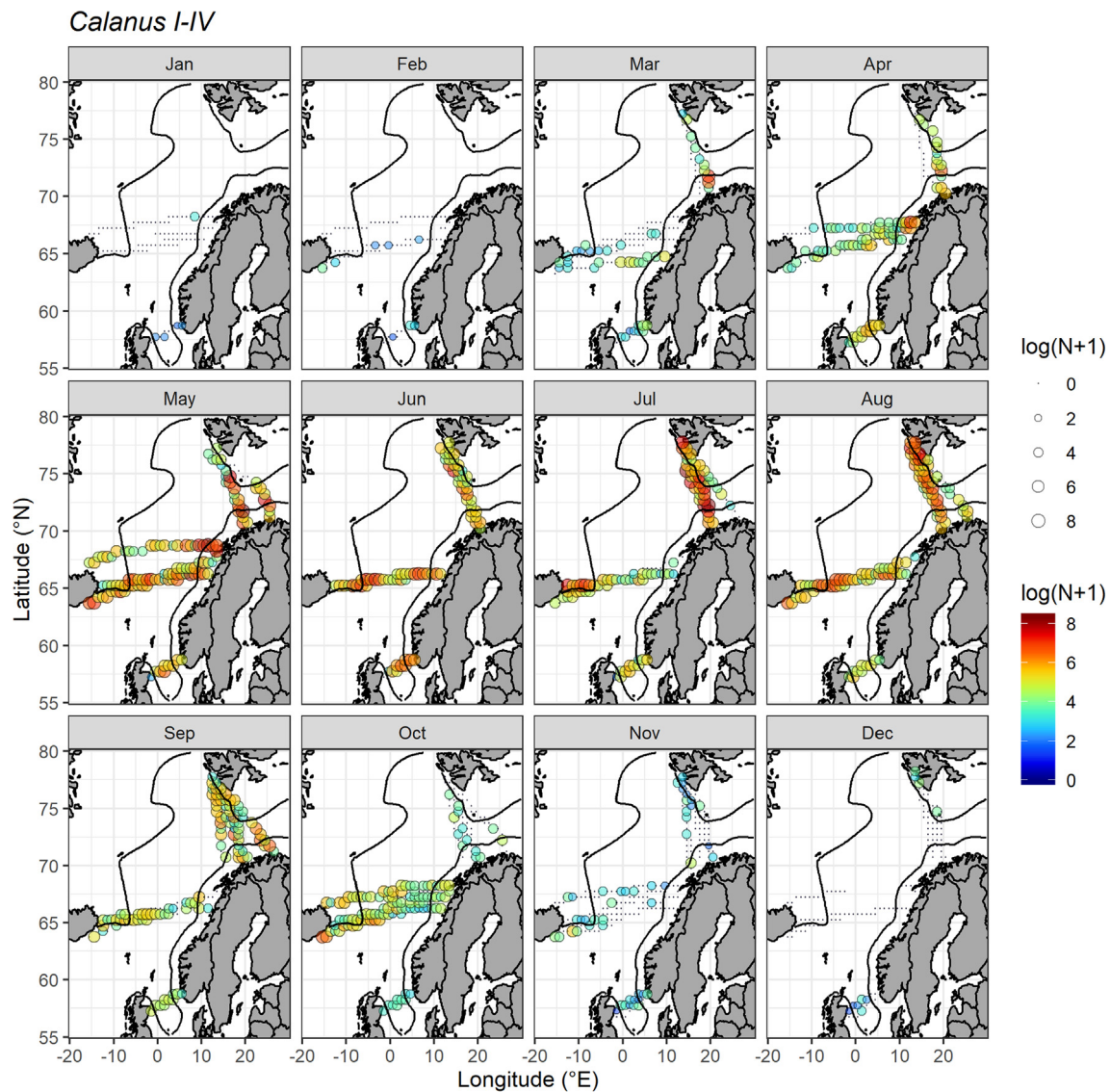


Fig. 6. Monthly abundance (\log_e scale) of *Calanus* spp. stages CI-IV per spatial grid cell along the three transects. Includes *C. finmarchicus*, *C. helgolandicus* and *C. glacialis*. The abundance represents the average count per sample, corresponding to ca. 3 m^3 . The contour line is set at salinity = 34.9.

while all three species co-occurred from April to June, where after *C. hyperboreus* disappeared from upper water masses while the two other species continued to coexist. Even in the arctic habitats, *C. finmarchicus* was the numerically dominant species.

3.2. Timing of *Calanus* spp.

The older stages of *C. finmarchicus* along the central transect displayed their first peak about one month earlier in spring in Atlantic than in Coastal water (Fig. 10). In Atlantic water, a first peak was observed in April, while in Coastal water the first peak was seen in May. In Arctic water, there seemed to be a prolonged peak from April to May. In Atlantic water, a second peak occurred in June, and what seem like a third but minor peak was indicated in October. In both Coastal and Arctic waters, secondary peaks were displayed in August, and in Coastal water a third peak was observed in October (Fig. 10).

Young copepodite stages of *Calanus* are not analysed to species, and it is therefore not clear which species that *Calanus* copepodites of stage I-IV in the different regions and water masses belong to. However, it is logical to believe that most of the young copepodites in a given region and water mass belong to the most abundant species for the older stages. Therefore, young stages along the central transect were most

probably *C. finmarchicus*. Along the central section, young stages appeared about one month earlier in Coastal than Atlantic and Arctic waters (Fig. 10). The first peak in Coastal water was registered in May, and in Atlantic and Arctic waters in June. While the peak dropped quickly in Atlantic water, the decrease was much slower in Arctic water. A second peak was clear in Atlantic water in August, while this was less clear in Coastal water. Still, during autumn, young copepodites were present in Coastal water in moderate numbers, and in higher abundances in Arctic water (Fig. 10).

Along the northern transect, the timing of appearance of older *C. finmarchicus* stages in spring resembled that of the central transect, though with no clear difference in timing in the Atlantic compared to the Arctic waters (Fig. 10). However, there seemed to be a lag in Coastal water. As for the central transect, the young *Calanus* stages there were probably mostly *C. finmarchicus*. Both in Atlantic and Coastal waters, the young stages displayed a first peak in May, followed by second peaks in July which was clearest in the Atlantic water. In Arctic water, the abundance of young stages increased steadily from May, reaching an annual peak in August. The timing of younger stages seemed somewhat delayed along the northern transect compared to the central transect, at least for the Coastal and Arctic waters (Fig. 10).

On the southern transect, older stages of *C. finmarchicus* were

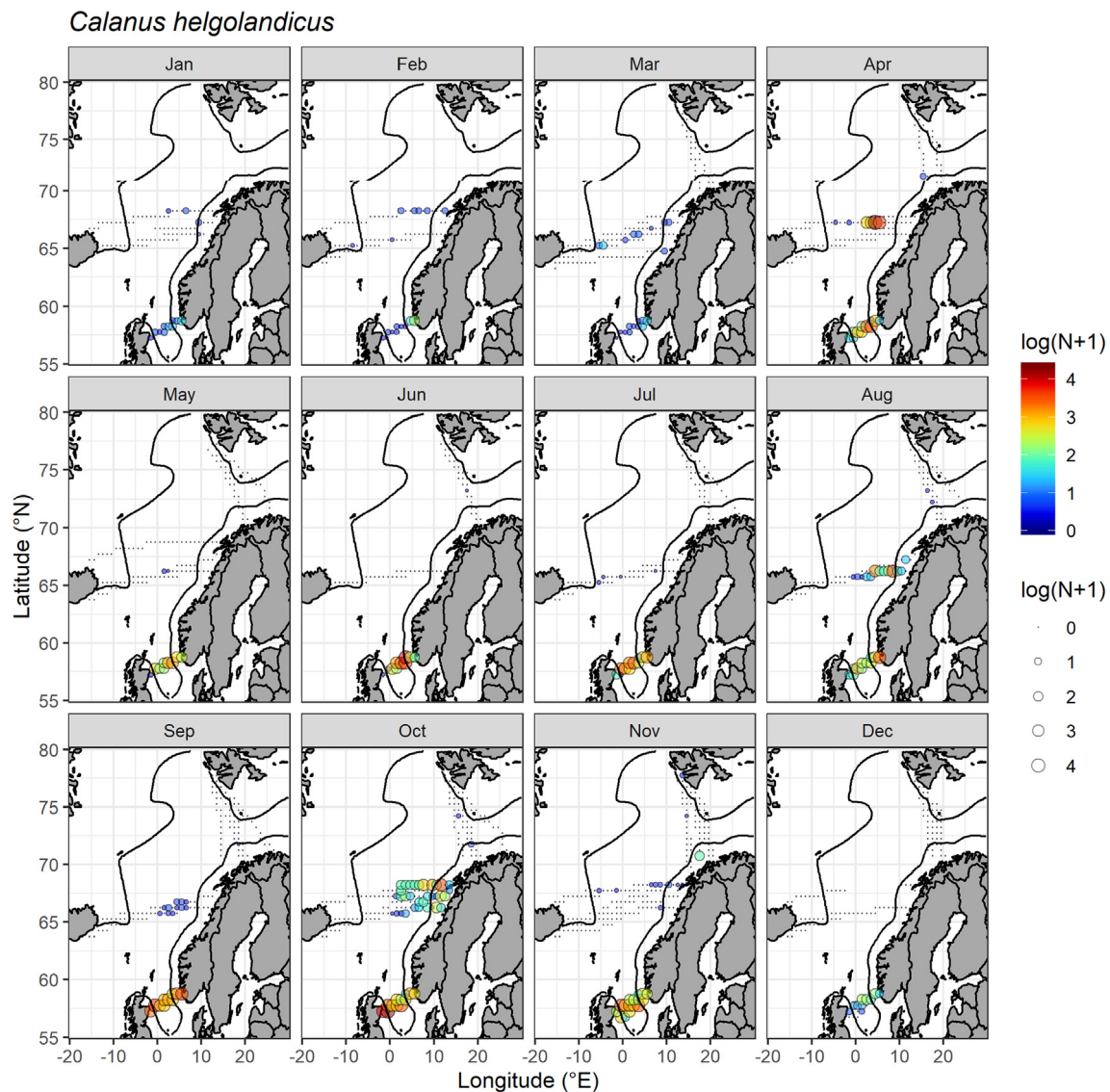


Fig. 7. Monthly abundances (\log_e scale) of *Calanus helgolandicus* (CV-CVI) per spatial grid cell along the three transects. The abundance represents the average count per sample, corresponding to ca. 3 m^3 . The contour line is set at salinity = 34.9.

present in rather low abundances most of the year, and particularly rare in the Coastal UK region during the first half of the year (Fig. 10).

Older stages of *Calanus helgolandicus* were predominantly observed on the southern transect, occurring in considerable abundances from April in the Coastal Norwegian and Atlantic waters, and without great changes during the rest of the year. In contrast, its abundance was low in the Coastal UK water until August, where after the numbers increased rapidly to reach an annual peak in October (Fig. 10).

The young stages along the southern transect may belong to both *C. finmarchicus* and *C. helgolandicus* as old stages of both species were present, but with the ratio of the two species changing during the year. Young stages were present along the southern section from about February to October, and most abundant in the Norwegian Coastal and Atlantic waters. In both these water masses the highest abundances were recorded in June. In the Coastal UK water, the very modest maximum was displayed as late as September (Fig. 10).

Older stages of *Calanus hyperboreus* were found mostly along the central transect. From being practically absent in winter, its abundance rose quickly from March, reaching a sharp peak in April, thereafter falling rapidly and being practically absent in upper waters from June and onwards. This species also occurred in lower numbers along the northern section in May and June, displaying a small peak in June

(Fig. 10).

Calanus glacialis almost exclusively occurred along the northern section, and with its highest abundances recorded in the Arctic water. The species displayed low abundances in both Arctic and Atlantic water in April. From May, its numbers rose quickly, reaching a sharp and moderate peak in Atlantic water in June, and a sharp peak with much higher abundances in July in the Arctic water. From September, the levels were low in all regions (Fig. 10).

3.3. Near-surface habitat temperatures of *Calanus* spp.

Near-surface temperatures for the different *Calanus* species were assessed from interpolated monthly temperature climatologies for depth of 30 m matching the time (month) and location (spatial grid cell) for each CPR sample (Fig. 11). We note that neither the sampling area nor depth covers the whole range of the environmental conditions experienced by the species throughout their spatial distribution or entire life cycle, for instance due to vertical migration behaviour including both diel vertical migration (DVM) and overwintering in deep waters. Hence, this assessment is restricted to the habitats in upper waters, and should be considered as a description of niche and not tolerance.

Calanus finmarchicus was observed with near-surface temperatures

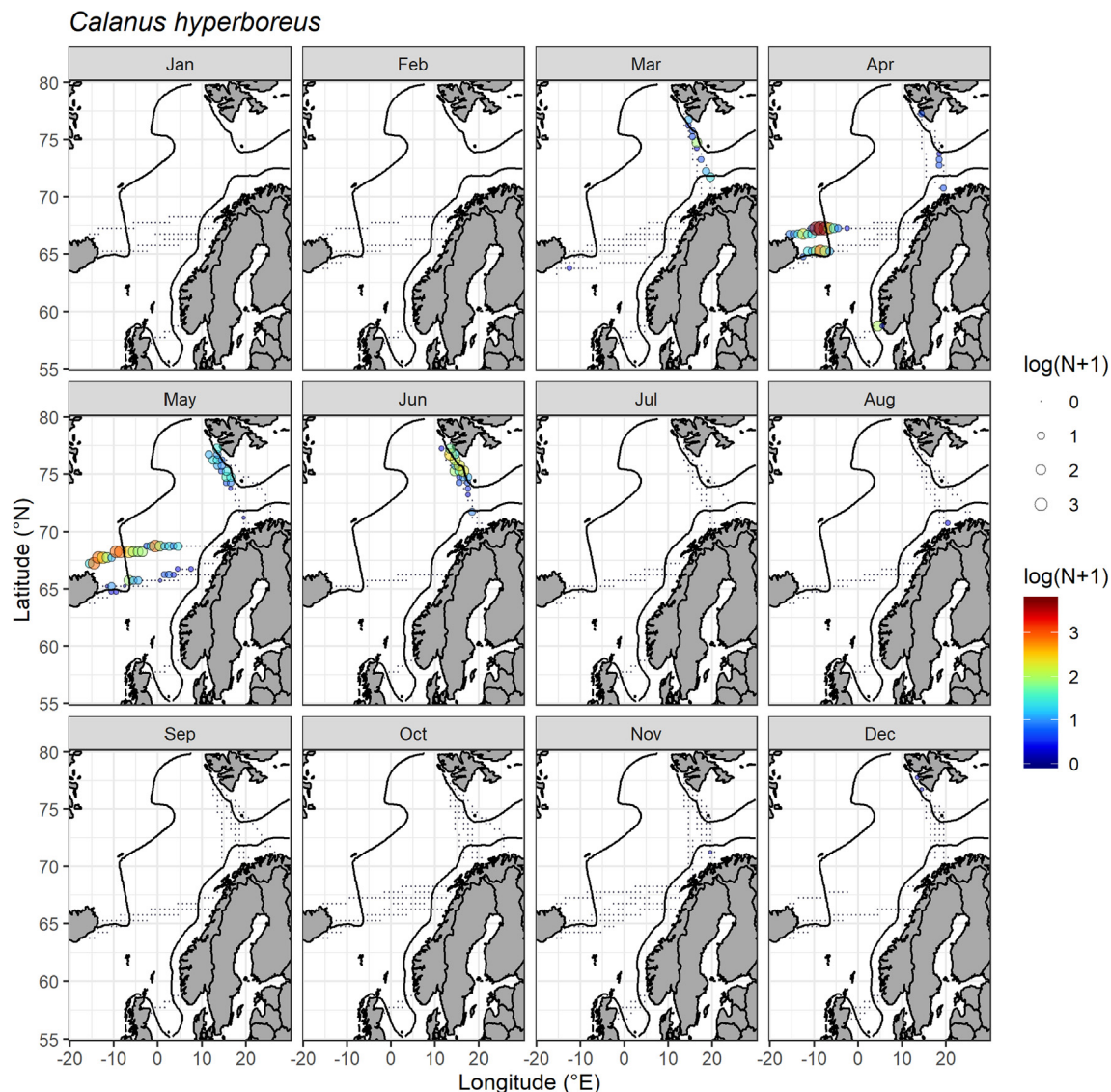


Fig. 8. Monthly abundances (\log_e scale) of *Calanus hyperboreus* (CV-CVI, but probably including some CIII-CIV too (see Richardson et al. (2006))) per spatial grid cell along the three transects. The abundance represents the average count per sample, corresponding to ca. 3 m^3 . The contour line is set at salinity = 34.9.

ranging between approximately 0–13 °C, with the highest abundances occurring between about 5–9 °C (Fig. 11). In Atlantic water, *C. finmarchicus* showed its maximum abundances between 5 and 10 °C (Fig. 11). In Arctic waters (considering both the northern and central transects), *C. finmarchicus* was observed between approximately 0–10 °C, with the temperature range being limited to about 2–6 °C along the northern section. In Coastal waters, the species occurred at temperatures between 4 and 13 °C.

Calanus helgolandicus abundances increased with increasing temperature in both Coastal and Atlantic waters (Fig. 11). It displayed strongly skewed distributions, with modes at about 13 °C, and long tails towards lower temperatures. In these water masses, the abundance of *C. helgolandicus* was generally low below about 6 °C, intermediate between around 6–9 °C, and comparatively high and strongly increasing when temperature passed about 10 °C.

Calanus hyperboreus showed a strong affinity for cold water, with the temperature range between approximately 0–7 °C. The distribution was strongly skewed, peaking between 0 and 2 °C, with a long tail towards higher temperatures (Fig. 11). In Arctic water on the western part of the central transect, where abundances were by far the highest, the temperature range was 0–3 °C, and the peak occurred between 0 and 2 °C. In the Arctic water along the northern transect, the temperature range

was shifted towards higher temperatures, 3–5 °C, and the peak at 4 °C. In Atlantic water, abundances were highest between 3 and 5 °C. The relationships between abundance and temperature for *C. hyperboreus* and *C. helgolandicus* were more or less inverse.

The range for the temperature distribution of *C. glacialis* was 0–7 °C, and the peak at 5 °C (Fig. 11). In Arctic water along the central transect, the species occurred in comparatively lower abundances at temperatures of approximately 0–2 °C, while in the Arctic water along the northern transect it occurred between about 2–6 °C, with a clear peak at 5 °C. *C. glacialis* was also present in relatively low abundances in Atlantic water at temperatures between 3 and 7 °C (Fig. 11).

Younger copepodites of *Calanus* spp. showed a relationship with temperature very similar to that of the older stages of *C. finmarchicus*. The shape of the distribution for young copepodites was unimodal, peaking between around 4–11 °C, but individuals were present within the whole temperature range. Some of the young copepodites found at high temperatures were probably *C. helgolandicus* (Fig. 11).

3.4. Abundance versus biomass of the *Calanus* species

For older stages of each of the four *Calanus* species, we estimated the approximate biomass per combination of transect, water mass and

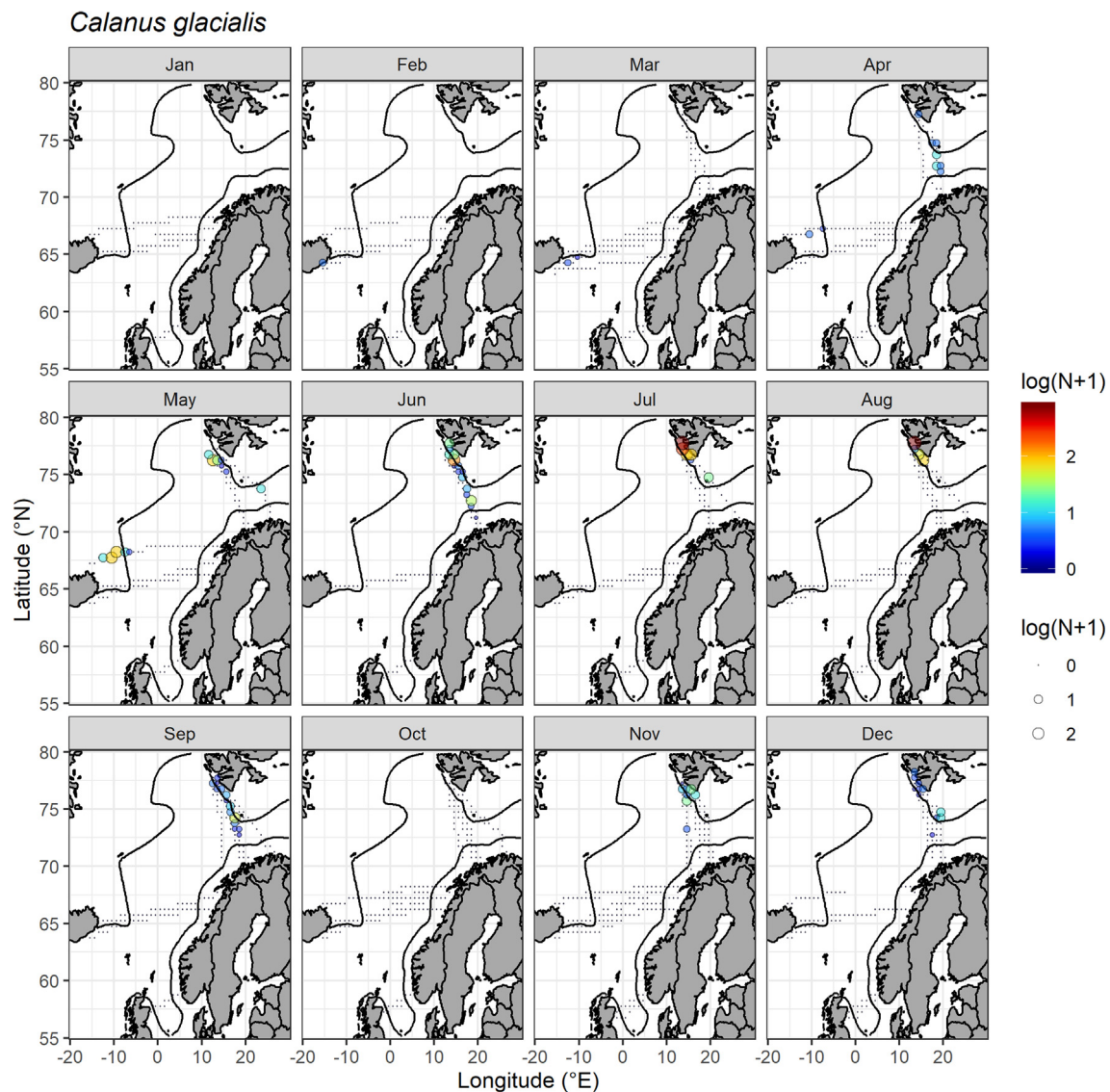


Fig. 9. Monthly abundances (\log_e -scale) of *Calanus glacialis* (CV-CVI) per spatial grid cell along the three transects. The abundance represents the average count per sample, corresponding to ca. 3 m^3 . The contour line is set at salinity = 34.9.

month (Fig. 12). *C. finmarchicus* generally dominated the *Calanus* biomass by far within the study area. Exceptions were *C. hyperboreus* in Arctic water in the Iceland and Norwegian Seas in spring and *C. helgolandicus* along the southern transect during much of the year, which could match or exceed the near-surface biomass of *C. finmarchicus* (Fig. 12).

4. Discussion

4.1. Older stages of *C. finmarchicus* and younger stages of *Calanus* spp.

We observed *C. finmarchicus* throughout the study area, with very low surface abundances of older stages from November through January, which coincides with its overwintering period (Sømme, 1934; Østvedt, 1955; Hirche, 1983, 1996). The main overwintering areas in the Northeast Atlantic are the deep basins in the Norwegian Sea. The overwintering population mainly consists of copepodite stage CV, but also some CIV's and adults (Østvedt, 1955; Melle et al., 2014). Termination of overwintering and ascent towards the surface layers takes place in late winter (Østvedt, 1955; Miller et al., 1991; Hirche, 1996; Heath, 1999), and increasing concentrations in the upper layers are typically noted from around February and during the following months

(Melle et al., 2014 and references therein). The CV's from the overwintering population (G0) moult to adults in early spring, and then reproduce. In spring and early summer, eggs and young individuals of the new generation of the year (G1) will appear (Niehoff & Hirche, 2000; Melle et al., 2004). This sequence of events was reflected in our dataset, where numbers of stage CV and adults increased in upper waters from February, reaching high abundances in April and May.

The presented CPR data demonstrated a strikingly late seasonal descent for at least parts of the *C. finmarchicus* population within Atlantic water masses in the Norwegian and Iceland Seas. High numbers of older stages of *C. finmarchicus* were observed in near-surface waters along the central transect as late as October (Figs. 4, 5). This observation is novel, as the general understanding is that most *C. finmarchicus* leave the surface layers in summer or early autumn to initiate overwintering in deeper waters. This observed pattern is consistent and not caused by one or two very high years, but rather a general trend of high *C. finmarchicus* abundance in Atlantic water on the central transect in October within the studied time period (Fig. 13).

Looking more closely into the data, it is apparent that *C. finmarchicus* is producing two generations per year in this area. This contradicts the general understanding that *C. finmarchicus* primarily has one annual generation in Atlantic water through its main distributional area, while

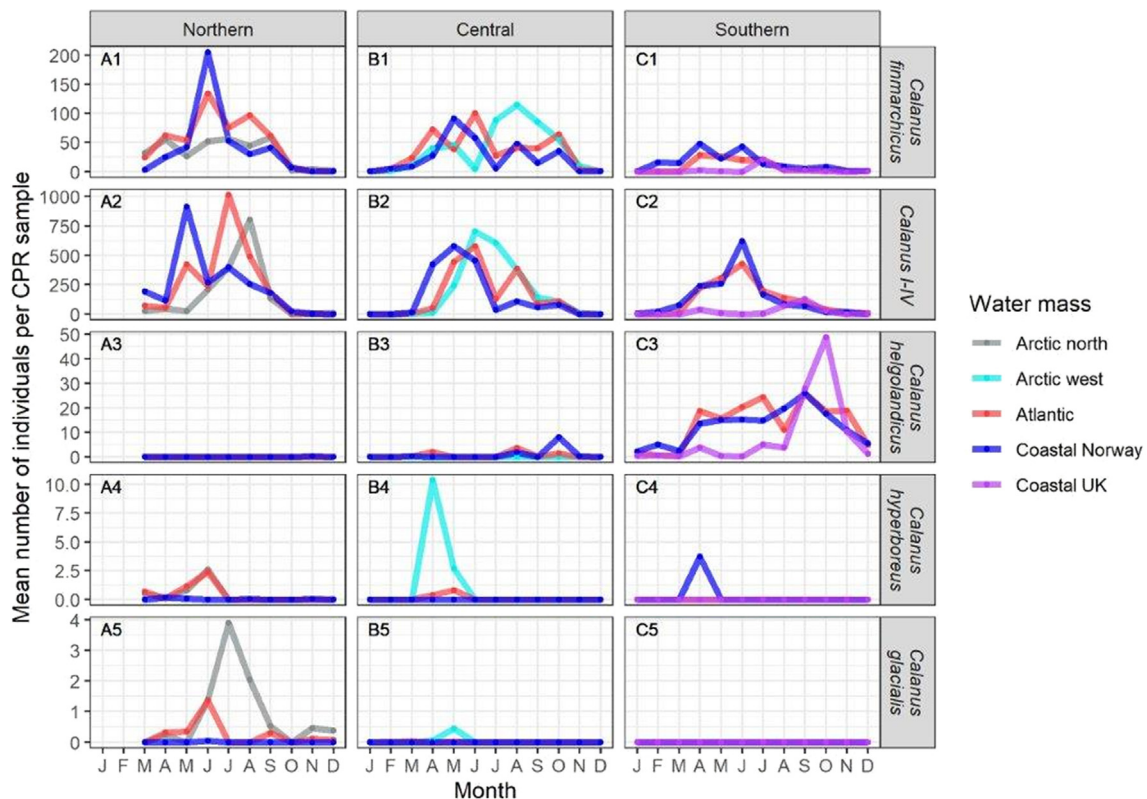


Fig. 10. Seasonal development of *C. finmarchicus* (CV-CVI), *C. helgolandicus* (CV-CVI), *C. hyperboreus* (CV-CVI but probably also some CIII-CIV), *C. glacialis* (CV-CVI) and young *Calanus* spp. (CI-CIV) at the southern, central and northern transects and the associated water masses. The x-axes show month and the y-axes represent mean number of individuals per sample. Note differing scales for y-axes.

a lifecycle of two generations per year is restricted to southern areas and Coastal waters (Melle et al., 2014, and references therein). We find that the G0 generation appears in March and April, and the young G1 is clearly present in May and June (Figs. 10 and 13). In June, G1 individuals have developed into adults, and by August a notable G2

generation is reflected by a new peak of young *Calanus* spp. stages. Two months later, in October, an adult G2 generation is evident (Fig. 13).

The high late-autumn concentrations of older stages in surface waters may be a feature that we simply have failed to notice until now. One explanation could be a general lack of sampling in that area late in

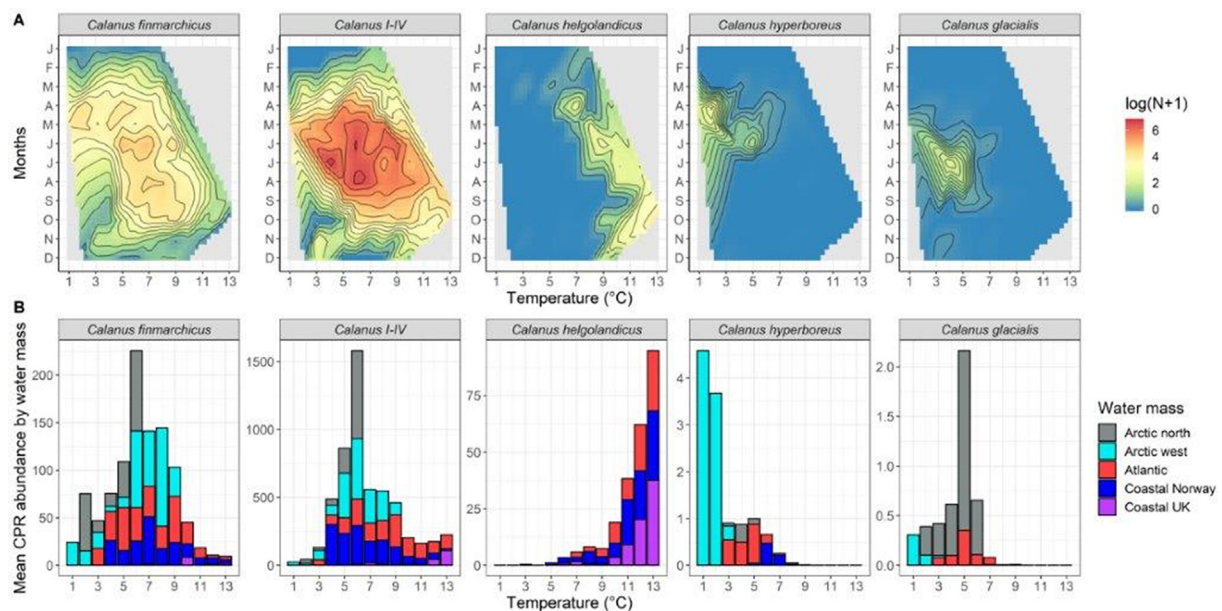


Fig. 11. Abundances of the different *Calanus* species (mean number of individuals per sample) versus temperature (°C). Older stages of *C. finmarchicus*, *C. helgolandicus*, *C. hyperboreus* (possibly including some CIII-CIV), *C. glacialis* as well as younger stages of *Calanus* spp. Only combinations for temperature-bin and water mass with 2 or more observations are used in the figure. Bars show mean abundances for each water mass, which are indicated with colours. Note differing scales for y-axes, and that summing up the abundances for the different water masses at a given temperature would not make sense due to stacked abundances.

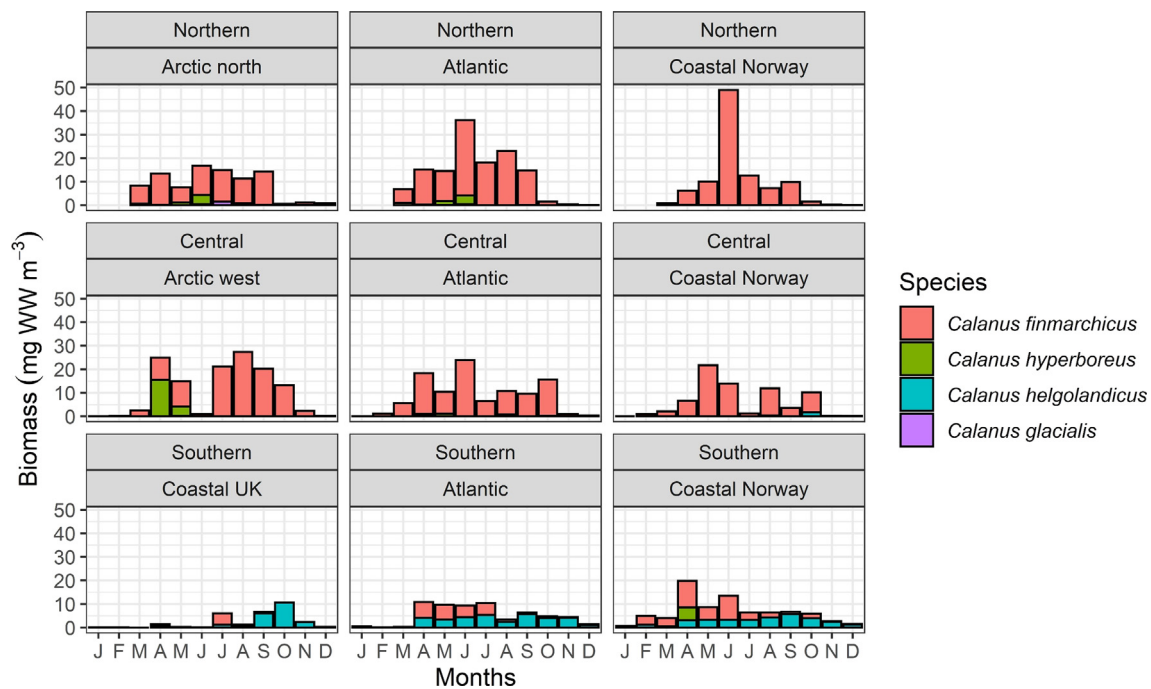


Fig. 12. Estimated average near-surface biomass (wet-weight, mg m^{-3}) of four *Calanus* species for different combinations of transect, water mass and month.

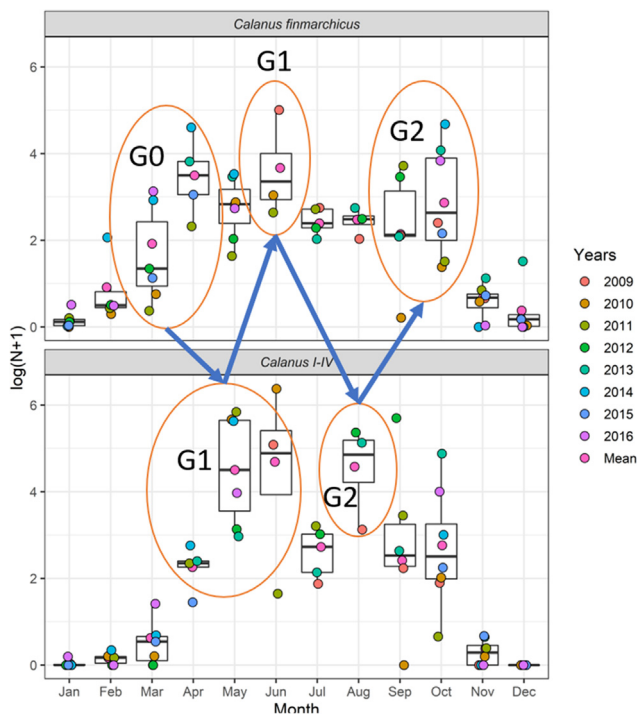


Fig. 13. Boxplot of monthly *C. finmarchicus* and *Calanus* I-IV abundances in Atlantic water on the central transect. All individual years and mean of all years plotted as points. The ovals and generations show our interpretation of the population development.

autumn. It is also possible that this finding may reflect a recent change in seasonality or population behaviour, and that the *C. finmarchicus* population to a larger extent may have completed a second generation in recent years. The CPR collects plankton from depth of around 7 m, which is much shallower than standard net samples, which are typically hauled vertically or obliquely between a certain lower depth and the surface. It might be that the CPR catches a specific subset of the population, e.g. individuals that choose not to descend – maybe due to

ambient feeding conditions, temperatures, or perhaps due to the individuals not being physiologically ready for overwintering (e.g. inadequate lipid reserves, c.f. Fiksen, 2000). Hence, these could be G2 individuals that are simply delayed, not yet having descended. Since we currently have no realistic means of estimating the relative importance of this upper component to the overwintering population, we cannot assess whether these high surface concentrations are important to the *Calanus* population as a whole. However, these individuals represent a potentially important food source to predators like larger zooplankton, fish and mammals in the area, and are therefore likely to be of ecological importance. Since *Calanus* is a central species in the ecology of the Norwegian Sea, changes in its annual cycle are likely to be important to other trophic levels. Therefore, the observation of highly abundant older stages of *C. finmarchicus* in upper waters late in autumn in the Norwegian Sea clearly warrants further studies.

For older stages of *C. finmarchicus*, there was no marked peak in the Coastal water along the central transect prior to the arrival of the young G1 stages in spring. The interpretation could be that a relatively low abundance of adults in the Coastal water, hence not visible as a peak in February or March, produced the G1 generation, or at least the first part of it. In that case, the peak of CV-adults in Coastal water around May, could in fact represent the G1 rather than the G0 population. In April, the abundances of younger stages of *Calanus* were quite high near the Norwegian coast on the southern and central transects, but less so in the north (Fig. 10). The young stages observed near the coast in April were considered to represent the new *C. finmarchicus* generation of the year. Along the central section, younger stages of *Calanus* appeared about one month earlier in the Coastal water than Atlantic water, while in the Arctic water the young copepodites seemed further delayed even if the time for the peak maximum was the same as for Atlantic water. At least two generations for the younger stages were evident in the Atlantic and Coastal waters, although for the latter region the distribution from August onwards was rather flat and without marked peaks. Only one generation was observed in Arctic water, and this peak was skewed and with a prolonged duration, indicating a slower rate of stage development in colder arctic water masses (Campbell et al., 2001). The number of generations in Coastal water is tricky to evaluate just from the older stages, as it lacks a marked increase or clear parent peak preceding the peak for the younger stages (Fig. 10). Likewise, Bagøien et al. (2012)

who analysed an independent dataset collected by WP2 and MOCNESS hauls, found a clear spring peak in young copepodite stages in Coastal water off mid Norway starting in April, but also there without a preceding marked increase of adult females. Some increases in CV's and adults were noted in that case, although very subtle compared to in the Atlantic and Arctic waters. The same pattern is observed in the present CPR data set, where the first low abundances for the group of older stages appear in February (approximately 1.5 ind. m^{-3}) while the first younger stage individuals appear in March (around 5 ind. m^{-3}) and April (around 140 ind. m^{-3}). The order of timing for the first new generation of the year for *C. finmarchicus* in the Norwegian Sea, starting first in Coastal water, then in Atlantic water, and apparently further delayed in the Arctic water has been proposed before, based on analyses of independent data (Broms et al., 2009; Bågøien et al., 2012). Along the northern transect the timing of the new generation peaked in May for both Coastal and Atlantic waters. More notable, the Arctic water on the northern section lagged far behind, with densities not reaching peak values before August. Along the northern transect, two generations are proposed from the peaks for the younger stages in May and July, for both Norwegian Coastal water and Atlantic water, with the second peak in Atlantic water being higher than the first peaks. In contrast, only one generation was observed in the Arctic water at that transect (Fig. 10). Based on model simulations, Skaret et al. (2014) predicted two distinct peaks in egg production in late April and late June in Atlantic water masses at the entrance of the Barents Sea. In that study, the second generations were larger than the first. This fits well, both numerically and time wise, with our findings (Fig. 10), with the time delay being explained by stage development time (Campbell et al., 2001).

The timing of generations for *C. finmarchicus* shown for the different water masses along the central section in this study generally agrees well with that previously reported for the same overall area in the Norwegian Sea. For Coastal water, a major and wide peak for younger stages was observed around May, while minor increases were observed for August and October. We believe that the May peak represents generation G1, and hypothesize that the small maxima in August and October might represent generations G2 and G3. Wiborg (1954) presented stage-composition for *C. finmarchicus* throughout the seasonal cycle at four stations off the Norwegian Coast in 1949 and 1950. The timing for stages CI-CIII described by Wiborg (1954) seems to agree rather well with the timing we report for *Calanus* stages CI-CIV in Coastal water on the central transect. The timing of the first two peaks around May and August for the CPR data also fit well with the results of Bågøien et al. (2012), who plotted seasonal development for the *Calanus* stages in different water masses in the Norwegian Sea, by pooling data from 1993 to 2008 for latitudes within $62\text{--}70^\circ\text{N}$. However, in their study the last maxima around October was absent. In Atlantic water along the central transect, younger stages peaked around June and August and remained present until October, and we interpret the two peaks as representing generations G1 and G2. This timing would be in agreement with the results of Østvedt (1955) and Melle et al. (2004) with both these studies performed at Weather Station Mike in the Norwegian Sea, as well Bågøien et al. (2012). However, while the central transect August peak in our CPR dataset was very clear and roughly about half the height of the June peak, the August peak for stages CI-CIII in Østvedt (1955) as well as in Bågøien et al. (2012) were notably less marked compared to the summer peaks. Østvedt (1955) noted a second spawning in August and September, and commented that this was not as prolific as the spawning in spring. In Arctic water along the central transect, the CPR data displayed younger stages peaking from about May to September, with its maximum occurring around June. The timing for the peak agrees well with the results of Bågøien et al. (2012) for the period from May to July, although in that dataset abundances after August were much lower.

Our data show *C. finmarchicus* occurring over the temperature range $1\text{--}13^\circ\text{C}$, and with abundances peaking between approximately $2\text{--}10^\circ\text{C}$. This is in accordance with the results of Bonnet et al. (2005), who

reported that this species occurs between 0 and 15°C , but with highest abundances between 0 and 9°C .

4.2. *C. helgolandicus*

C. helgolandicus primarily occurred along the southern transect, which agrees well with what we know about its main distribution area. This represents the more temperate northern North Sea, occupied by Atlantic water masses and hosting the pseudo-oceanic temperate species *C. helgolandicus* and the subarctic species *C. finmarchicus* (Beaugrand et al., 2002; Bonnet et al., 2005). Along with warming seawater during recent decades, this area has changed from being considered the southern border for the distribution of *C. finmarchicus* and mainly occupied by *C. finmarchicus*, to become more dominated by *C. helgolandicus* (Beaugrand et al., 2002; Bonnet et al., 2005). *C. helgolandicus* has been documented to occur from the Mediterranean in the south to the North Sea and southern Norwegian Sea (Bonnet et al., 2005), and is even registered as far north as at the entrance to the Barents Sea (Dalpadado et al., 2012).

In the northern North Sea, the present analysis showed that *C. helgolandicus* may not be the typical autumn-species previously suggested for this area (e.g. Bonnet et al., 2005), as high surface concentrations were recorded also during spring. *C. helgolandicus* in both Atlantic and Norwegian Coastal waters was as abundant in spring as autumn. Bonnet et al. (2005) presented seasonal patterns for *C. helgolandicus* in different regions, and divided the results into 3 main groups with differing seasonality (see their Fig. 5). Our CPR data would represent Boxes 1 and 2 in their Fig. 2, which were characterized by *C. helgolandicus* occurring mainly in autumn. While this would match very well the coastal water near the UK, the Atlantic water and coastal Norwegian water clearly had an earlier timing starting in spring, which Bonnet et al. (2005) reported as typical in more southerly areas, and further speculated might be related to temperature conditions. However, further north in the Norwegian Sea, the highest abundances of this species in our study were observed in autumn, probably reflecting transportation time with northward currents from the southern core regions in addition to the species timing.

Our data showed increasing abundances of *C. helgolandicus* with temperature up to 13°C , which was our temperature maximum. This concurs with the conclusions of Bonnet et al. (2005), that this species generally occurs in waters with temperatures between 9 and 20°C with peak abundances between 13 and 17°C .

4.3. *C. hyperboreus*

The main production area of *C. hyperboreus* in the Northeast Atlantic is believed to be in the Greenland Sea (Hirche, 1991), where the population can be retained within the Greenland Sea Gyre. However, when water masses are shed from this gyre and move downstream and southward into the Iceland Sea and further east into the Norwegian Sea (Fig. 2), significant numbers of *C. hyperboreus* can be transported to adjacent areas (Hirche, 1997; Kristiansen et al., 2019). This would explain why we observed the highest abundances of *C. hyperboreus* in Arctic water masses in the Iceland Sea. The central CPR transect does not always follow the exact same route every month. It is interesting to note that few *C. hyperboreus* were found when the transect followed a more southern route and thus sampling in water masses with mainly Atlantic origin, while transects with a slightly more northern path recorded higher numbers in water masses with Arctic origin (Figs. 1 and 8). Equal amounts of *C. hyperboreus* were found in the Atlantic and Arctic waters south and west of Svalbard, with almost identical numerical and temporal patterns (see Figs. 4 and 8). Whether these specimens originated in the arctic Barents Sea or have crossed the polar front from the Greenland Sea cannot be determined on basis of the presented data. This is due to both the limited geographical area covered, and the possibility of misclassified or truly mixed water masses.

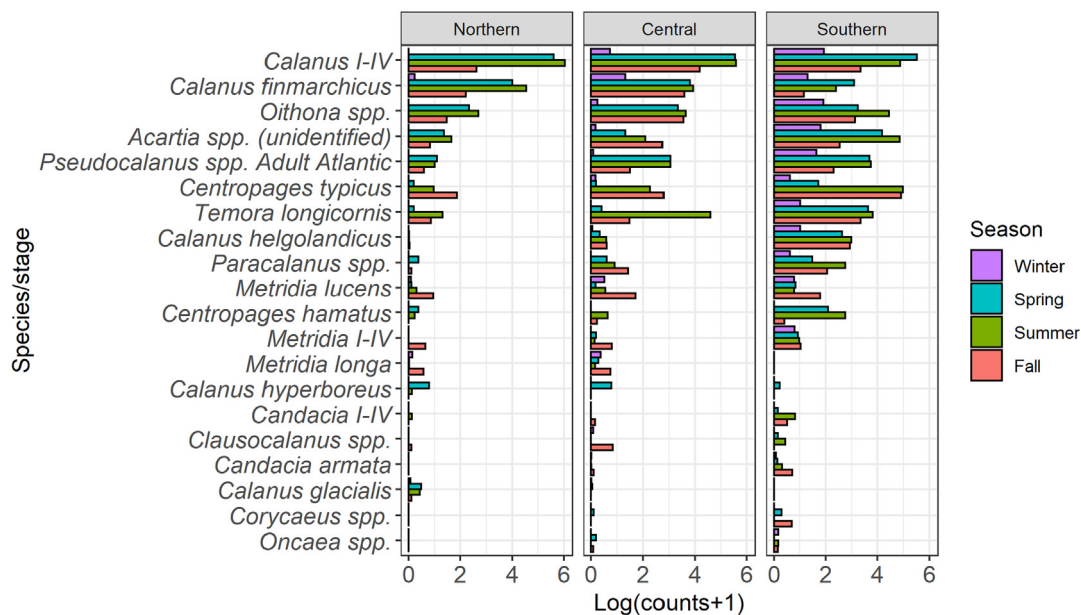


Fig. 14. Average abundances (\log_e -counts per sample) of dominant zooplankton taxa. Each transect is shown in a separate panel, with colour representing seasonal period. The seasonal periods are here defined as winter (15th Dec–14th Mar), spring (15th Mar–14th Jun), summer (15th Jun–14th Sep) and fall (15th Sep–14th Dec). All water masses are here combined. See Richardson et al. (2006) for which stages that are included in each taxon.

C. hyperboreus generation time is reported to vary from 1 to 4 years, with the longer generation times generally found in Arctic water. Like the other *Calanus* species in the area, *C. hyperboreus* undergoes seasonal vertical migrations and spends winter diapausing at depth. The main overwintering areas for *C. hyperboreus* are subject to marked annual and inter-annual variations in ice cover, which affects phytoplankton growth, timing, and consequently food availability. The variability in sea ice cover and timing of open waters periods may impact the timing for seasonal vertical migrations for *C. hyperboreus* (Falk-Petersen et al., 2009). The CPR data provide no information about vertical distributions and stage composition during winter, but due to the high frequency sampling effort, determining the timing for when the adults reach surface waters after their seasonal ascent is possible. In Arctic water in the Iceland Sea, *C. hyperboreus* showed a very distinct peak and was only found for a short period in surface water, as they started to ascend into surface water in March and April, peaked in April, and disappeared from surface water at the end of May. This is in accordance with Hirche (1997) who reported that ascent in the Greenland Sea Gyre and West Spitsbergen Current is in April. Our data from the West Spitsbergen Current are less clear, indicating that some individuals appear as early as March but with a peak occurrence in June. This could possibly be an effect of interannual variation as the results of Hirche (1997) are based on one single year of sampling (1989), while the CPR data presented here span the period 2008 to 2016.

Even within the Arctic water masses around Iceland, *C. finmarchicus* is more numerically dominant than *C. hyperboreus* in spring. However, due to the large size difference between the two species, *C. hyperboreus* is the dominating species in terms of biomass (Fig. 12). Norwegian springspawning herring (*Clupea harengus*) enters the Arctic front at this time of year during their annual feeding migration in the Norwegian Sea (Misund et al., 1997) and *C. hyperboreus* have been found to be the most important prey in April in Arctic water (Dalpadado et al., 2000). Later in the season and in Atlantic water, *C. finmarchicus* is more dominating in the diet. This could be due to the short period that *C. hyperboreus* spends feeding at surface waters (Fig. 8) and could potentially be a strategy to limit predation risk after the herring arrives in the area (c.f. Kaartvedt, 2000).

4.4. *C. glacialis*

C. glacialis only occurred in small numbers along the northern transect, and almost exclusively in the Arctic water masses with a peak abundance in July. This fits well with previous observations from vertically integrated net samples from the northern and eastern Barents Sea (Aarflot et al. 2018). Even though *C. glacialis* is an arctic species, the highest average observations in surface waters occurred at a temperature around 5 °C. Others have previously reported decreasing *C. glacialis* biomasses with increasing temperature, with the highest biomasses occurring in water temperatures close to 0 °C (Daase et al., 2007; Aarflot et al., 2018). However, the Arctic water along the northern transect is likely to be somewhat mixed with the warmer Atlantic water, and thus our data on *C. glacialis* numbers versus temperature could be interpreted as representing the higher end of its temperature niche. In any case, in water masses with temperature above 7 °C we found no *C. glacialis* in any samples.

Only low numbers of *C. glacialis* were found in the Atlantic water masses along the northern transect. This makes sense as the species is described as an arctic shelf species, and considering that the Atlantic water there is a comparatively warm water mass with a southerly origin that enters the area after passing over the deep ocean basins of the Norwegian Sea.

On the central transect towards Iceland, observations of *C. glacialis* were made only on the most northerly stations in water masses classified as arctic (Figs. 1 and 9). *C. glacialis* is not a dominating species in the Iceland Sea, and encounters with this species are most frequent in the northern parts of the Iceland Sea (Gislason & Silva, 2012).

C. finmarchicus and *C. glacialis* are considered indicator species for Atlantic and Arctic waters, respectively, with both playing key ecological roles in their respective environments. Morphologically the species are very similar, and the most common way to distinguish between them is by individual size within developmental stage. This method is used for separating the two species in the CPR samples presented here. Some recent studies have indicated that this may lead to erroneous classification of the two species, due to some overlap in the size-distributions for a given stage (Lindeque et al., 2006; Parent et al., 2011; Gabrielsen et al., 2012; Choquet et al., 2018). It is beyond the scope of this paper to evaluate potential misclassification of these two species in

question, apart from mentioning the possible shortcoming of the pro-some length method for species-differentiation.

4.5. Dominant copepod species apart from *Calanus* spp.

A list of numerically dominant copepod taxa was compiled to provide a general description of the copepod community in the different areas, and to put the abundance of the four *Calanus* species in context (Fig. 14). Comparatively fewer species were strongly dominating in the northern area, while the total abundance within the dominant taxa combined increased southwards. The cyclopoid copepod *Oithona* spp. (comprising all copepodite stages) was very common along all sections from spring to autumn, particularly along the central and southern transects. *Acartia* spp. (all copepodite stages), *Pseudocalanus* spp. (adults), *Centropages typicus* (all copepodite stages) and *Temora longicornis* (all copepodite stages) were very numerous along the southern transect and decreasing northward, from spring to autumn. *Paracalanus* spp. (all copepodite stages) and *Metridia lucens* (stages CV-CVI) were numerous along the southern transect, present in moderate numbers along the central transect, and much sparser along the northern transect. *Centropages hamatus* (adults) was abundant along the southern transect (Fig. 14). *Metridia longa* (stages CV-CVI) occurred in rather low numbers along the central and northern transects in autumn, and was practically absent from the southern transect. *Clausocalanus* spp. (adults), *Candacia armata* (CV-adult), *Candacia* stages CI-CIV, *Corycaeus* spp. and *Oncaea* spp. (all stages) were included at the end of the shortlist of numerically dominant species

4.6. Looking forward

The two main reasons for focusing on *C. finmarchicus* and its congeneric relatives *C. helgolandicus*, *C. glacialis* and *C. hyperboreus* in this study is that they are numerically dominant zooplankton species representing a large biomass in the Northeast Atlantic while also occupying distinctive thermal preferendums and niches. As such, these species can act as useful indicators and ‘sentinel’ species to environmental changes and in particular highlight the consequences of climate warming in this region. These species are also very useful as indicator species for marine management and policy (Edwards et al., 2010). By far the most numerically dominant species, *C. finmarchicus*, shows the most cosmopolitan thermal envelope for this region ranging between 0 and 10 °C with an optimum of around 5–6 °C. The more southerly distributed and temperate species *C. helgolandicus* has a thermal preferendum ranging between 9–18 °C with a thermal optimum of 11 °C (Helaouët et al., 2013). In the North Sea *C. finmarchicus* is at its southern edge and *C. helgolandicus* is close to its optimum (Helaouët et al., 2013). For the arctic species, *C. glacialis*, the thermal range was between 0 and 7 °C and the larger and lipid rich species *C. hyperboreus* shows a strong affinity towards more polar waters with a thermal range between 0 and 5 °C and a thermal optimum towards the lower end of this range. As thermal boundaries shift northward due to climate warming it is expected that the more southerly species *C. helgolandicus* will become more dominant. This phenomenon has already been recorded with the warming of the North Sea over the last 50 years, shifting the numerical dominance of the subarctic *C. finmarchicus* to the temperate species *C. helgolandicus*. The subarctic species *C. finmarchicus* has declined by over 70% in the North Sea since the 1960s.

C. hyperboreus has its main distribution centre in the Greenland Sea (Hirche 1991), and in the present study this species was mainly recorded downstream in the Iceland Sea and western part of the Norwegian Sea. This species is strongly associated with southward flowing Arctic water in the Greenland and Iceland Seas (Kristiansen et al., 2019), separated from the Atlantic domain by the Arctic Front. It is, however, challenging and beyond the scope of this work to speculate about how the distribution of this species in the northern regions will become affected by climate warming, since changes in the properties

and distributions of intermediate and deep waters in the Fram Strait is linked to the circulation patterns with the Eurasian Basin of the Arctic Ocean (Langehaug & Falck, 2012). The uncertainty regarding *C. hyperboreus* distribution in a warming world has previously also been noted by others (Renaud et al. 2018 and references therein).

C. glacialis mainly occurred in Arctic water on the northern transect. During the last decades, the temperature in the Barents Sea has increased, and increasingly large parts of the Barents Sea are now covered with Atlantic water and less with Arctic water, and the level of ice cover has decreased strongly (ICES, 2018). As *C. glacialis* is an arctic shelf species, also related to the ice, there is a concern that this species may experience hard times and decline in the Barents Sea. Our northerly transect in this study does not cross the core of the main distribution area for this species, but due to the current systems around Svalbard, it should still contain signals regarding the effects of climate change on this species in the Barents Sea and adjacent areas (c.f. Dalpadado et al., 2012). A major concern is that subarctic species may over time replace the arctic species and that this may represent a large decrease in overall biomass due to the general understanding of Arctic species being larger and even having an unproportionally higher lipid content (c.f. Søreide et al., 2010, Daase et al., 2013). Changes in biomass levels and reductions of these lipid sources are expected to have large implications for higher trophic levels (Søreide et al., 2010). However, the effect of borealization of the Barents Sea, with *C. finmarchicus* replacing the shelf species *C. glacialis* is presently debated (Renaud et al., 2018). These authors argue that lipid storage is closely related to size, and that the species overlap in size. Furthermore, their model results suggest that shorter generation time and population turnover rate may compensate for the reduction of the larger species *C. glacialis* and *C. hyperboreus* in the Barents Sea in terms of available lipids in the ecosystem. Another concern is that different species may have different seasonality's, which may also be affected by environmental factors such as temperature. Hence, even if the *Calanus* biomass level was to remain unchanged, a change in seasonality due to changing species composition or environmental factors, might impact the temporal match with predators higher up in the food net, and hence be of strong importance for the ecosystem.

The new northern Norwegian routes were initially established due to these rapid changes to plankton and climate and the movement of plankton northwards observed over the last 50 years in the subpolar Atlantic. These rapid changes in plankton were originally observed in the North East Atlantic where most of the CPR routes operate, with plankton northerly movement measured at about 23 km per year in this region (Beaugrand et al., 2009). To continue these observations of rapid biological movement and biodiversity changes it was considered crucial to establish more northerly CPR routes covering the Nordic Seas to continue to document these changes as well as to monitor for possible trans Arctic migrations.

With the Norwegian CPR tows now having been operating for over 10 years in Nordic waters the CPR survey adds to and complements other monitoring methods by providing a broader spatial and temporal perspective. Most other surveys are coastal, and many of these are sampled less frequently than the CPR routes. The CPR survey also adds value by providing multi-decadal data at the Atlantic basin scale that can help disentangle and interpret changes observed in the Nordic Seas and help predict changes over the next coming decades. For example, regions that currently support Arctic ecosystems might instead support sub-Arctic systems within the next 10–20 years, if not sooner. The biological signals of change we see further south in Atlantic sub-polar systems now can be used to detect the early warning signs of change in the Arctic.

4.7. Main findings

C. finmarchicus clearly displays two generations in Atlantic water and one generation in Arctic water over a large area covering the

Norwegian Sea, eastern Iceland Sea, and at the entrance to the Barents Sea. This is somewhat in contrast to the general understanding, where *C. finmarchicus* is considered to have primarily one generation in Atlantic water through its main distributional area and that a lifecycle of two generations per year has been restricted to southern areas (Melle et al., 2014, and references therein).

In the northern North Sea along the southern transect, *C. helgolandicus* was present in relatively high numbers from April to November along the Norwegian Coast and in Atlantic water masses, contradicting the general notion that this species is mainly an autumn species in this area (Bonnet et al. 2005). Along the UK coast however, *C. helgolandicus* was much more numerous in the autumn compared to the rest of the year. Furthermore, *C. helgolandicus* was found on the central transect in both Coastal and Atlantic water, and registered as far north as the entrance to the Barents Sea.

C. hyperboreus was most numerous in near-surface water during a few spring months in Arctic water masses in the Iceland Sea, while *C. glacialis* was numerous in Arctic water masses on the northern transect in July. The upper limit of the temperature niche for both these Arctic species was found to be around 7 °C.

Declaration of Competing Interest

The authors declared that there is no conflict of interest.

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