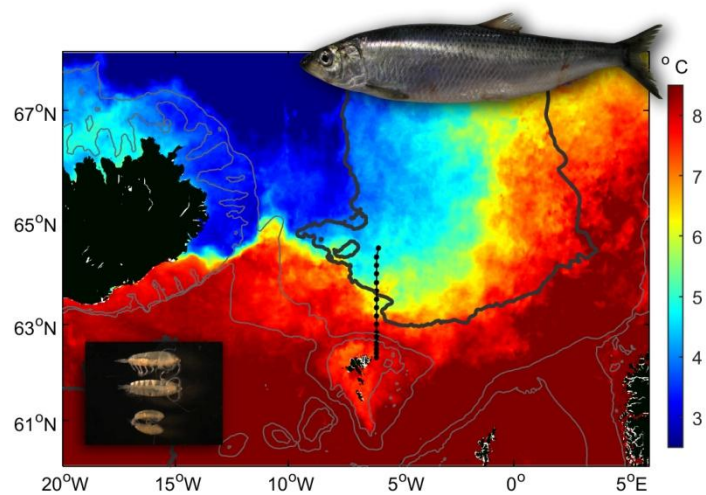


PhD Thesis

**Population dynamics of *Calanus* species within the southwestern Norwegian Sea - links to water mass distribution and Norwegian spring spawning herring**

Inga Kristiansen



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## Preface

This work has been carried out at the Faroe Marine Research Institute (Havstovan) in Tórshavn, Faroe Islands and is the basis for the dissertation for the degree of philosophiae doctor (Ph.D.) in marine biology at the University of the Faroe Islands (Fróðskaparsetur Føroya).

The thesis is divided into four chapters. The first chapter introduces the topic and background information that forms the study as well as the objectives and goals. The second chapter briefly shows the data material used. The results and discussion are merged together in the third chapter. Here, the papers do not follow a chronological order as the essence of the findings are brought forward and discussed. Finally, a short list of the main findings and new questions that have arisen as a result of this study, which remain to be addressed, are summarized in the final chapter. The last part of thesis contains the five papers. At the time of submission, four papers were accepted and one paper was a manuscript draft.

## List of papers

- Paper I Kristiansen, I., Gaard, E., Hátún, H., Jónasdóttir, S., Ferreira, A. S. A. 2016. Persistent shift of *Calanus* spp. in the southwestern Norwegian Sea since 2003, linked to ocean climate. ICES J. Mar. Sci. 73, 1319–1329. [doi:10.1093/icesjms/fsv222](https://doi.org/10.1093/icesjms/fsv222).
- Paper II Kristiansen, I., Hátún, H., Petursdottir, H., Gislason, A., Broms, C., Melle, W. *et al.* 2019. Decreased influx of *Calanus* spp. into the south-western Norwegian Sea since 2003. Deep. Res. Part I 149. [doi:10.1016/j.dsr.2019.05.008](https://doi.org/10.1016/j.dsr.2019.05.008).
- Paper III Kristiansen, I., Jónasdóttir, S. H., Gaard, E., Eliassen, S. K., and Hátún, H. 2021. Seasonal variations in population dynamics of *Calanus finmarchicus* in relation to environmental conditions in the southwestern Norwegian Sea. Deep Sea Res. Part I, [doi:10.1016/j.dsr.2021.103508](https://doi.org/10.1016/j.dsr.2021.103508).
- Paper IV Kristiansen, I., Hátún, H., Eliassen, S.K., Jacobsen, J.A., Gaard, E. and Petursdóttir, H. 2021. Spatial variability of the feeding conditions for the Norwegian spring spawning herring in May. Draft.
- Paper V Cisewski, B., Hátún, H., Kristiansen, I., Hansen, B., Larsen, K.M.H., Eliassen, S.K. and Jacobsen, J.A. 2021. Vertical migration of pelagic and mesopelagic scatters from ADCP backscatter data in the southern Norwegian Sea, *Frontiers in Marine Science*, [doi:10.3389/fmars.2020.542386](https://doi.org/10.3389/fmars.2020.542386).

## Abstract

The copepods *Calanus finmarchicus* and *C. hyperboreus* are the ecological most important copepod species in the Nordic Seas and key links between the lower and higher trophic levels. Population dynamics of these *Calanus* spp. were studied in relation to environmental factors, water mass distribution and predator-prey interactions, with a particular focus on the southwestern Norwegian Sea. This region is characterized by inflow of warm and saline Atlantic Water from the southwest and cold and less saline East Icelandic Water, of Arctic origin, from the northwest, that meet and establish the Iceland Faroe Front (IFF). Time series of the *Calanus* spp., in May and September, and co-collected hydrographic data, spanning from early 1990s to 2020, were used in our analyses, in combination of larger spatio-temporal hydrographic and zooplankton data sets of the Norwegian Sea and eastern Iceland Sea.

The IFF separates the *Calanus* spp. into two distinct populations. The overwintered *C. finmarchicus* individuals recorded south of the IFF are smaller, contain less wax esters and are less efficient in reproduction compared to individuals who overwinter north of the IFF. Prior to 2003, the numbers of overwintered *C. finmarchicus* individuals dominated north of the IFF while newly produced individuals dominated south of the IFF, in May. In 2003, an abrupt change in *C. finmarchicus* stage composition occurred within the subarctic region, north of the IFF, from being dominated by overwintering stages in May to an increased abundance of young stages from the new generation. Concurrent with the earlier occurrence of young stages in May, there was also a shift in production of a single generation per year to two generations per year after 2003. Thus, the shift around 2003 resulted in similar phenology as south of the IFF. A comparable post-2003 reduction within the subarctic region is observed in the abundance of *C. hyperboreus* and in the total zooplankton biomass in spring within the EIC, coinciding with an abrupt reduction in volume of Modified East Icelandic Water (MEIW) in the intermediate layers. This suggests that the abundance of *C. hyperboreus* can be used as a biological indicator for a change in water mass distribution.

The association was less clear between the volume of MEIW and the abundance of overwintered *C. finmarchicus* individuals. This is probably due to its increased abundance in both the Norwegian and Iceland Sea. However, since 2015 the *C. finmarchicus* stages within the subarctic region has reverted back towards the state prior to 2003, which strongly suggests that *C. finmarchicus* is also influenced by the variable volume of MEIW.

On the annual research cruise in May 2020, high abundances of *C. hyperboreus* and overwintered stages of *C. finmarchicus* were found northwest of the Faroe Islands, overlapping the high aggregations of adult herring, on their feeding migration, within the same region. During low influx years of MEIW (2007-2011) showed that less *C. hyperboreus* was found in the herring diet. In contrast, in 2020, which was a high influx year, herring had fed more intensely on *C. hyperboreus*. This suggests that the transport of MEIW is important for the abundance of *Calanus* spp. as prey for Norwegian spring spawning herring within the Norwegian Sea.

### Føroyskur samandráttur (Faroese abstract)

Stórar nøgdir av reyðæti (*Calanus finmarchicus*) eru í Norskahavinum og hetta ætið er høvuðsføði hjá teimum stóru ferðandi stovnunum av norðhavssild og makreli, sum koma til havøkið norðanfyri Føroyar um várið og summarið at finna føði. Seinastu árinu eru broytingar hendar í hesi pelagisku vistskipan. Endamálið við hesari verkætlanini var at fáa betri kunnleika til liviumstøðurnar hjá reyðætinum, ið eru tengdar at havfrøðiligum viðurskiftum, gróðrinum í sjónum og ávirkanin av uppsjóvarfiski, sum etur reyðæti. Verkætlanin hevur givið eina betri heildarfatan av hesum samanspælinum, m.a. hvussu liviumstøðurnar eru í heitum Atlantssjógvi og í køldum subartiskum sjógvi, og hvønn týdning havfrøðiligar broytingar kunnu hava á bæði reyðæti og sild.

Havøkið norðan fyri Føroyar er sermerkt av einari samanrenning ímillum heitan Atlantssjógv og kaldan sjógv frá Íslandsstreymunum sum elvir til Íslandsfrontin. Síðan 1993 hevur Havstovan gjørt árligar havfrøðiligar og lívfrøðiligar kanningar eftir standardskurði (Skurður N), har tann sunnari parturin umboðar heitan Atlantssjógv, og tann norðari parturin umboðar kaldan subartiskan sjógv. Kanningarnar benda á, at Íslandsfronturin skilur reyðætið í tvær ymiskar populatióner, og liviumstøðurnar í hesu báðum økjum eru rættiliga ymiskar. Yvirvetrandi reyðæti sum rekur tvørtur um sunnara part av Skurði N er smærri, hevur minni av lýsi, og gýtur minni í ovaru lögnum, í mun til reyðæti sum yvirvetrar norðanfyri Íslandsfrontin.

Áðrenn 2003, var meginparturin av reyðætinum í tí norðara partinum av skurði N í mai vaksin djór frá árinum fyri, og bert heilt frá yngri djór frá sama vári. Men í 2003 hendi ein broyting, soleiðis at meginparturin var yngri djór frá sama vári meðan munandi færri vóru frá árinum fyri. Í sama tíðarskeiðinum minkaðu nøgdirnar av tí størri artiska reyðætinum, *Calanus hyperboreus*. Líknandi broytingar í biomassanum av djóraæti vóru eisini at síggja eystanfyri Ísland. Kanningar vísa, at tey tíðarskeiðini, tá nógvur kaldur subartiskur sjógvur rekur úr útnyrðingi inn okkara øki norðanfyri, ávirkar tað bæði liviumstøðurnar hjá reyðæti og flytir eisini nógv *C. hyperboreus* í føroyskan sjógv. Og tey tíðarskeið, tá hetta kalda rákið er veikari, rekur samsvarandi minni av *C. hyperboreus* inn í føroyskt havøki. Hetta sambandið bendir á, at *C. hyperboreus* kann verða brúkt sum indikator fyri broytingum í havumhvørvinum á okkara leiðum norðanfyri. Síðan 2015 er bæði havfrøðiliga og nøgdirnar av báðum *Calanus* sløgnum aftur farin at líkjast støðuni áðrenn 2003.

Høvuðsføðin hjá sildini er vaksin individir av *C. finmarchicus*, av tí at mest er til av hesum slagnum. Tó tekur sildin heldur størri og føðsluríkari slagið, *C. hyperboreus*, tá tað er í umhvørvinum. Á árligu rannsóknarferðini í mai 2020, vóru tær størstu nøgdirnar, bæði av *C. hyperboreus* og vaksnum *C. finmarchicus* máldar ein útnyrðing úr Føroyum, júst har sum stórar nøgdir av vaksnari sild er at finna. Árinu 2007-2011, sum høvdu minni ávirkan av MEIW, vísti at minni av *C. hyperboreus* var staðfest í magakanningum. Hinvegin, í 2020, tá meira var av MEIW, hevði sildin eisini etið meira av *C. hyperboreus*. Hetta vísur at kaldur Íslandssjógvur hevur týdning fyri nøgdirnar av føði hjá norðhavssild norðan fyri Føroyar, og í Norska-havinum sum heild.

## **Acknowledgements**

First and foremost, I would like to thank my supervisors, Dr. Eilif Gaard, Dr. Hjalmar Hátún and Dr. Sigrún H. Jónasdóttir. Your guidance, enthusiasm and patience have encouraged and helped me through this project.

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During my studies I have been blessed with wonderful colleagues, who have also helped in various ways and taught me about topics previously unknown to me – thank you very much. I would especially like to thank my co-worker, Sólvá Jacobsen, who throughout these years has also become my friend, and with whom I always can turn to for stimulating discussions and, perhaps more importantly, vent out any frustrations.

The scientific material used in this study has been collected over many years. The effort many people have put into this work is greatly appreciated.

I would also like to extend my gratitude to the sources that have funded this project. These include the Danish Government, which has funded this work via the research program “Marine Climate in the North Atlantic and Its Effects on Plankton and Fish”, to the Faroese Pelagic Organization and Fisheries Research Fund of the Faroe Islands.

Finally, I would like to thank my wonderful family for your unlimited help and support.

Tórshavn, May 2021  
Inga Kristiansen

## Abbreviations

Table 1. Abbreviations of commonly used names in the thesis.

Acronym	Name
CTD	Conductivity, Temperature, Depth
EGC	East Greenland Current
EIC	East Icelandic Current
EIW	East Icelandic Water
FAMRI	Faroe Marine Research Institute
FC	Faroe Current
FSC	Faroe Shetland Channel
GSR	Greenland Scotland Ridge
G <sub>0</sub>	Overwintering generation of copepods
G <sub>1</sub>	New generation of copepods
IESNS	International Ecosystem Surveys in the Nordic Seas
IFF	Iceland-Faroe Front
IFR	Iceland-Faroe Ridge
JMF	Jan Mayen Front
JMR	Jan Mayen Ridge
MEIW	Modified East Icelandic Water
MNAW	Modified North Atlantic Water
NAO	North Atlantic Oscillation
NNAW	North Norwegian Atlantic Water
NSAIW	Norwegian Sea Arctic Intermediate Water
NSG	Norwegian Sea Gyre
SPG	Subpolar gyre



## 1 Introduction

The Norwegian Sea is rich in zooplankton and attracts large amounts of planktivorous fish. Key pelagic fish stocks perform their annual, large-scale migration to this region to feed on zooplankton during spring and summer, before continuing towards their winter area and spawning grounds (Fig. 1). This includes Norwegian spring spawning herring, mackerel and blue whiting, which are commercially and economically important fish stocks for the coastal states in the Northeast Atlantic.

During the feeding season, herring is the first pelagic stock to enter the Norwegian Sea and performs an east to west migration, navigating from lower to higher prey biomass. Since 2003-2005, an increasing amount of herring has been aggregating within the southwestern Norwegian Sea for a prolonged period during spring, summer and even autumn.

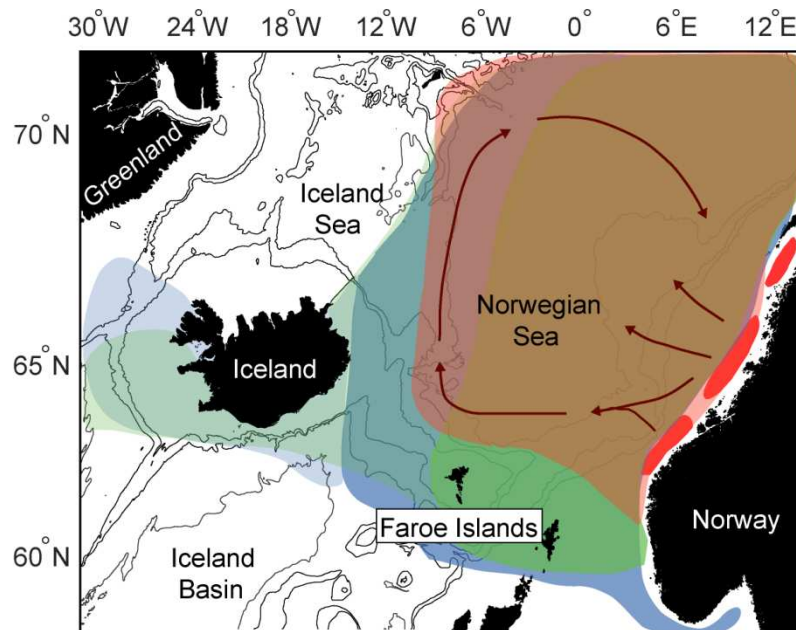


Fig. 1. Approximate summer feeding areas of the pelagic stocks: herring (red), mackerel (green) and blue whiting (blue), representing the period from the mid 1990s to present. The lightly shaded area indicates maximum concentrations. Spawning regions of herring are shown with red ovals along the Norwegian shelf.

The copepods, *Calanus finmarchicus* and *Calanus hyperboreus* are major prey species within the feeding region. In the Norwegian Sea, *C. finmarchicus* dominates the zooplankton community, both in terms of abundance and biomass (Wiborg, 1955; Strand et al., 2020). *C. finmarchicus* is also amongst the most numerically abundant copepods in the neighbouring Iceland Sea, but there its co-generic species, *Calanus hyperboreus*, dominates in terms of biomass. Soon after the post-2003 increase in pelagic stocks within the southwestern Norwegian

Sea, the zooplankton biomass in May within the wider region of the Norwegian Sea as well as the adjacent Iceland Sea started to decline to historically low values (ICES, 2020). This may be due to predation, but other factors can also be important. As copepods migrate vertically from dormancy at depth to the surface in spring/summer, individuals are transported with upper, intermediate and deeper water masses, depending on the species and season. Changes in water mass distribution may therefore affect zooplankton populations in terms of abundance and composition as well as the suitable habitat for fish populations. The association between ocean climate, zooplankton population dynamics and zooplankton as prey for herring are not fully understood and remain to be clarified. This is the focus of this thesis.

## 1.1 Oceanographic overview

### 1.1.1 Circulation pathways of upper layer water masses

The Nordic Seas, which comprise the Greenland, Iceland and Norwegian Seas, are separated from the rest of the other North Atlantic basins by the Greenland-Scotland Ridge (Fig. 2). The region is characterized by a poleward flow of warm and saline Atlantic water along the eastern part and a southward flow of cold and low-saline polar water along the western side (Helland-Hansen and Nansen, 1909). Within this region, the circulation and distribution of water masses is generally steered by the topographic margins and steep ridges that separate the basins (Poulain and Warn-Varnas, 1996).

The Atlantic inflow, which is the northern limb of the North Atlantic current system carries Modified North Atlantic Water (MNAW; Fig. 3a; Hansen and Østerhus, 2000) into the upper layers in the Norwegian Sea through the Faroe Shetland Channel (FSC), across the Iceland-Faroe Ridge and with a weaker branch through the Denmark Strait (Fig. 2). North of the Faroe slope, the warm current conveys this warm and saline water further east within the Norwegian Sea and subsequent northwards. Off approximately mid Norway, a fraction recirculates in the Norwegian Basin and is transformed into the Norwegian North Atlantic Water (NNAW) that flows southwards along the Jan Mayen Ridge (JMR) (Hansen and Østerhus, 2000).

From the Iceland Sea, the East Icelandic Current (EIC) transports colder and fresher East Icelandic Water (EIW) into the southwestern Norwegian Sea. The EIW is composed by polar water from the East Greenland Current and the Atlantic water entering the Iceland Sea through the Denmark Strait as well as waters modified through winter mixing and air-sea interactions within the Iceland Sea (Fig. 2). Farther east, off the Icelandic north-eastern slope, the EIW meets the northwestern flank of the warmer and more saline MNAW. This confluence establishes the Iceland-Faroe Front (IFF; Fig. 3a and 3b). A border zone is also created between the colder arctic water within the Iceland Sea and the warmer Atlantic water within the western Norwegian Sea by the Jan Mayen Front (JMF). While the northern frontal region is more or less fixed by the

JMR, the frontal position in the south can show relative large longitudinal shifts due to the variable volume of EIW carried by the EIC (Read and Pollard, 1992; Blindheim et al., 2000).

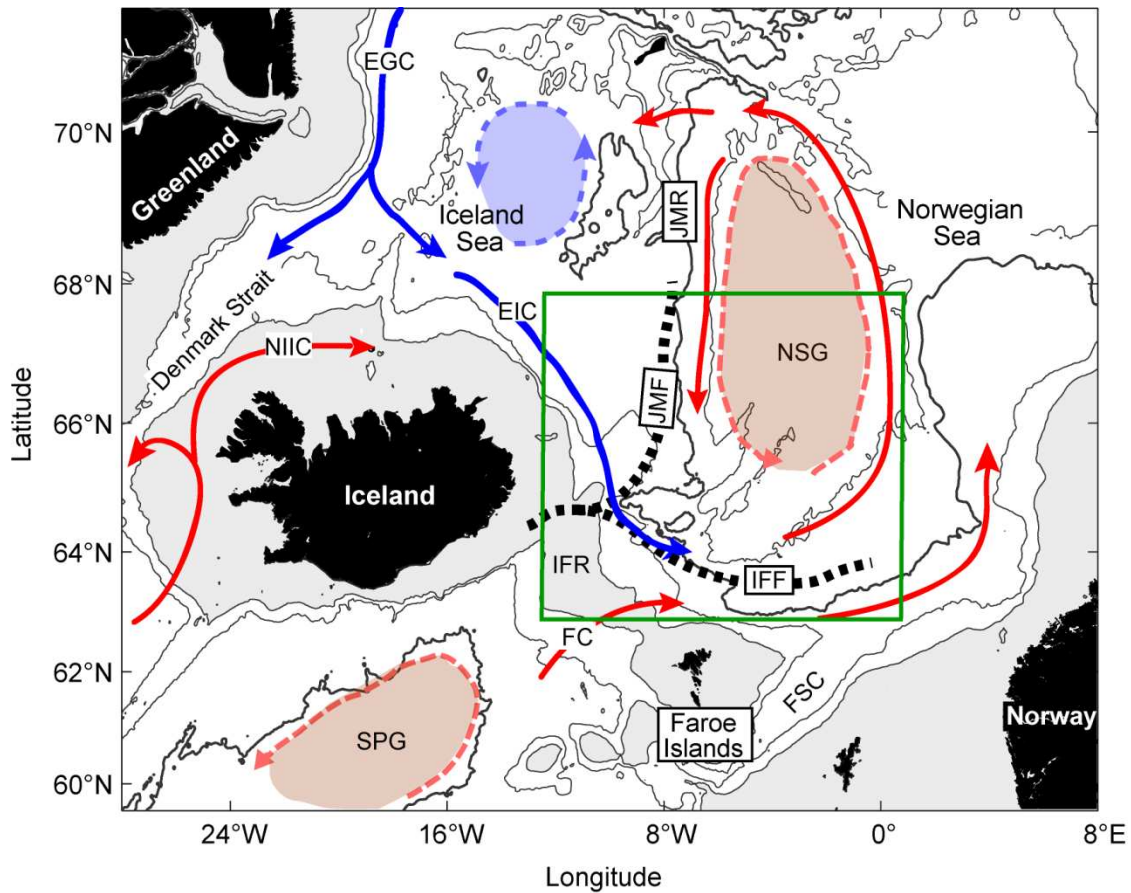


Fig. 2. Map of the wider study area and its surroundings. The main upper layer currents - warm (red) and cold (blue) - that influence the wider study area (green box) are displayed. Dotted black lines represent major fronts and dotted arrows illustrate the anticlockwise circulation of the gyres. The Greenland-Scotland Ridge is presented in light grey and the 500, 1000, 2000 (bold), and 3000 m isobaths are shown. See Table 1 for abbreviations.

### 1.1.2 Water mass distribution within the southwestern Norwegian Sea

As the MNAW is transported cyclonically within the Norwegian Basin (Poulain and Warn-Varnas, 1996), it continuously becomes cooler, fresher and denser through air-sea interactions and eventually submerges underneath the upper layer as the NNAW, approaching the northern Faroe slope (Fig. 3a and 3b; Read and Pollard, 1992).

Off the northeastern Icelandic shelf edge, the EIW slides isopycnally underneath the northward flowing MNAW. Further east, the southward flowing NNAW submerges under the EIW and is wedged between the EIW and MNAW. Extensive mixing between these water

masses creates the Modified East Icelandic Water (MEIW), of which the EIW is the main contributor. The MEIW is seen as a cold and fresh tongue sliding gradually at increasing depths along the IFF, passing the north of the Faroe slope and entering the southwestern Norwegian Sea and extending eastwards into the FSC (Read and Pollard, 1992) as an intermediate water mass (Blindheim et al., 2000).

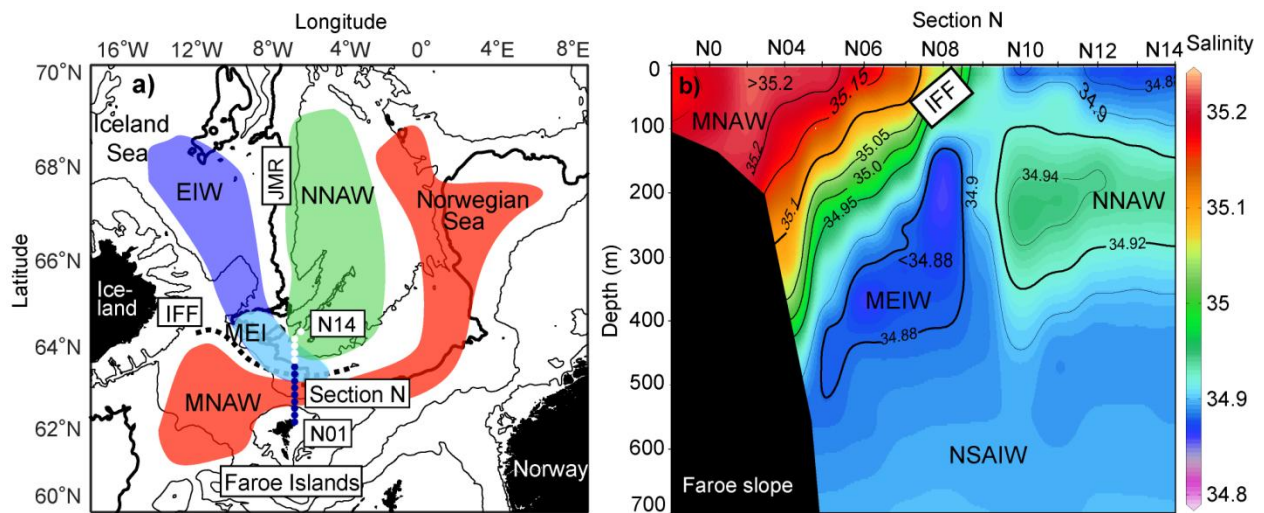


Fig. 3. Water masses that influence Section N. a) Water mass distribution within the upper 400 m and b) the average salinity distribution (1997 to 2001), which characterize the water masses along Section N. The subarctic sampling sites along Section N in (a) are shown in white (stations N10-N14) while the Atlantic and frontal stations are shown in blue (N01-N09). The 200, 1000, 2000 (bold), and 3000 m isobaths are displayed in (a). See Table 1 for abbreviations.

### 1.1.3 Influence of atmospheric circulation

Major shifts in water mass transport have taken place in the Norwegian and Iceland Sea since the early 1990s. These shifts are ultimately driven by atmospheric variability (e.g. Blindheim et al., 2000; Serra et al., 2010). Distribution of water masses is regulated by the strengthening and weakening of the anticlockwise circulation within the deep basins in the Norwegian and Iceland Sea, as well as the subpolar Atlantic (Fig. 2), which in turn is regulated by the prevailing wind pattern (Blindheim et al., 2000; Serra et al., 2010; de Jong et al., 2018). Parameters that often capture these processes are sea level pressure and sea surface height (Jakobsen et al., 2003; Richter et al., 2012; Holliday et al., 2020) which indices such as the North Atlantic Oscillation (NAO) and the subpolar gyre index are based upon (Hurrell, 1995; Hátún et al., 2005).

The early 1990s and 2000s are periods characterized with particularly strong and weak wind forcing, causing accelerated and decelerated circulation, respectively, of the Norwegian Sea Gyre (NSG; Chafik et al., 2020) and the subpolar gyre (SPG; Hátún et al., 2005). In 2003, the

circulation of the gyres was particularly weak. The weakened NSG, as a consequence of weaker wind forcing over the Nordic Seas (Hátún and McClimans, 2003; Richter et al., 2012), reduced the eastward transport of the EIW and MEIW into the Norwegian Sea (Blindheim et al., 2000; Serra et al., 2010). Simultaneously, the weakening of the SPG lead to stronger contribution of water masses of subtropical origin, and thus a sharp increase in temperature and salinity in the Atlantic water advected across the Greenland-Scotland Ridge, which propagated further throughout the Nordic Seas (Malmberg and Valdimarsson, 2003; Drange et al., 2005; Hátún et al., 2005; Holliday et al., 2008; Richter and Maus, 2011; Larsen et al., 2012). These cascading events coincide with record high sea surface height within the southeastern Norwegian Sea, which in turn reflects less EIW (Richter et al., 2012) and a more westward positioning of the JMF (Blindheim et al., 2000).

Fluctuations in water mass distribution and circulation patterns seem to be of large ecological importance as they may shift ecological boundaries, from primary via secondary productivity to a number of ecologically and economically important marine populations (Blindheim et al., 2000; Holst et al., 2002; Ji et al., 2010; Hátún et al., 2016).

## 1.2 Biological overview

### 1.2.1 Phytoplankton production

The seasonal cycle of *C. finmarchicus* production is related to the phytoplankton production (Broms and Melle, 2007; Bagøien et al., 2012). The timing of phytoplankton production in the Norwegian Sea differs between the water masses due to a difference in the build-up of the near-surface stratification (Bagøien et al., 2012), which is a prerequisite for a marked spring bloom to occur. The primary production generally starts in near-shore waters in the eastern Norwegian Sea and is progressively delayed with increasing distance from the coast (Broms and Melle, 2007). However, geographical variations of the bloom timing do occur as a result of water masses with different hydrographic features. Due to an earlier stratification, and thus a rapidly shallowing of the mixed layer, north of the IFF, the bloom onset within this region is initiated around the same time as within the Norwegian coastal areas (Bagøien et al., 2012; Zhai et al., 2012), suggesting better feeding conditions for *C. finmarchicus* earlier in the season.

### 1.2.2. *Calanus* spp.

The zooplankton biomass that is mainly represented by the *Calanus* spp. within the Iceland Sea (Gislason and Silva, 2012) and Norwegian Sea (Strand et al., 2020) is highest in the west and progressively reduces towards the Norwegian coast in May (Fig. 4). The lowest zooplankton biomass is within the Atlantic region, south of the IFF.

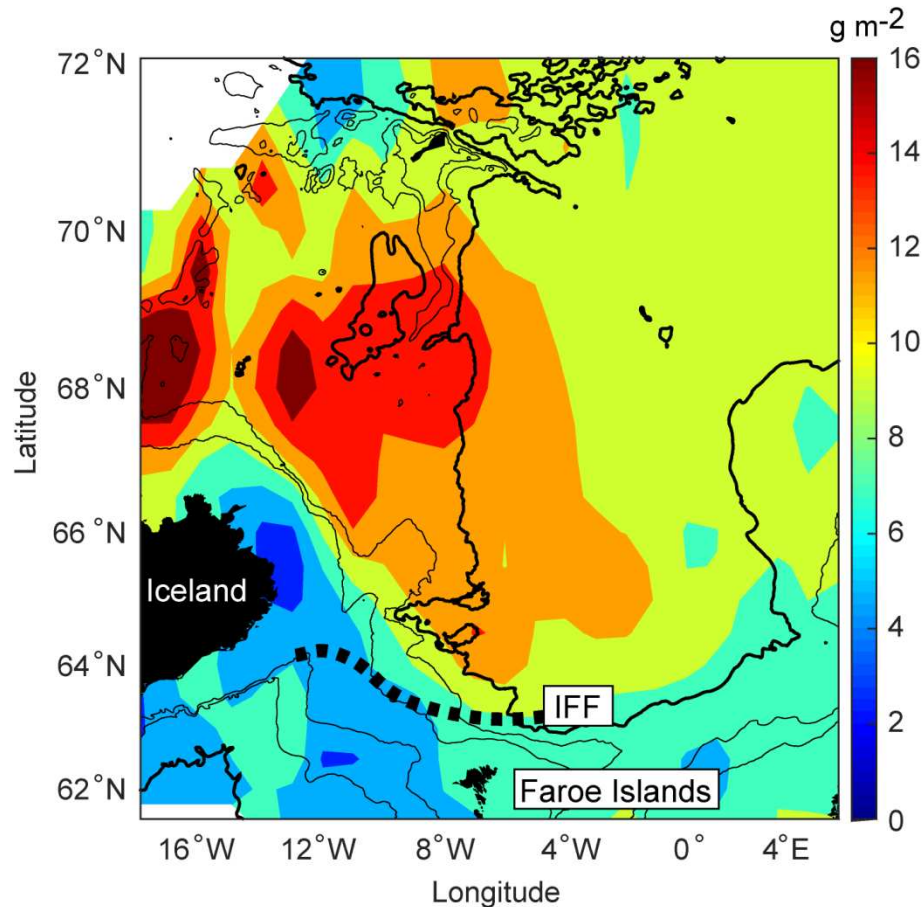


Fig.4. Zooplankton biomass from the International Ecosystem Survey in the Norwegian Sea and the eastern part of the Iceland Sea (IESNS) in May. Mean biomass in the upper 200 m, from 1998 to 2016. The 500, 1000 and 2000 (bold) m isobaths are shown. The Iceland-Faroe Front (IFF) is illustrated with the thick dashed curve.

### *Calanus finmarchicus*

Ascent from great depths is initiated in late winter/early spring and the overwintered generation ( $G_0$ ) moults into adults (C<sub>VI</sub>) and spawns within the upper layers. When spawned, the copepod develops through six naupliar and copepodite stages (C<sub>I</sub>-C<sub>VI</sub>). Individuals feed on the phytoplankton spring bloom, which is the main energy source that fuels egg production (e.g. Gaard, 2000; Jónasdóttir et al., 2008). However, the accumulated lipid reserve from the previous feeding season is also assumed to be an important energy resource immediately after ascendance. The juvenile stages (C<sub>IV</sub>-C<sub>V</sub>) assimilate food that is increasingly channelled toward building up the lipid energy reserves required to sustain the animals during the overwintering period (Jónasdóttir et al., 2015). In late summer, within the eastern and southern Norwegian Sea, a fraction of stage C<sub>V</sub> remain in the upper layer to moult into adults (C<sub>VI</sub>) and produce a second generation ( $G_2$ ). In contrast, in the Iceland Sea only one generation is evident (Strand et al.,

2020) and the juveniles (mainly stage CV) descend to depth where they overwinter (Heath et al., 2000a) at low metabolic rates (Ingvarsdóttir et al., 1999; Jónasdóttir et al., 2008).

Dense concentrations of overwintering individuals are found within the deep Norwegian Basin, mainly between 600 and 1200 m depth (Heath et al., 2000b). Individuals within the anticlockwise circulation of the NSG appear to be relatively self-contained (Heath et al., 2000b). Deep water currents control the distribution of the animals during diapause (Søiland and Huse, 2012) but during ascent, the distribution is determined by the Atlantic water current system. The southwestern Norwegian Sea receives direct arctic water influx from the Iceland Sea, where *C. finmarchicus* is amongst the most numerical copepod species (Gislason and Silva, 2012) where they exhibit a rather shallow overwintering depth ranging between 200-600 m (Gislason, 2018). Jointly these regions expel their water masses (Blindheim et al., 2000; Hansen and Østerhus, 2000; Chafik et al., 2020) and copepods (Helland-Hansen and Nansen, 1909; Heath and Jónasdóttir, 1999) into the FSC, which is also identified as one of the most populated overwintering areas (Heath et al., 2004).

### *Calanus hyperboreus*

Within the Iceland Sea, the larger *C. hyperboreus* is the dominating species in terms of biomass (Gislason and Silva, 2012; Gislason, 2018). *C. hyperboreus* has a centre of abundance in the Greenland Sea (Conover and Corner, 1968; Hirche, 1997) and likely enters the Iceland Sea through a smaller artery that branches off from the East Greenland Current (Fig. 2; Astthorsson and Gislason, 2003). It is adapted to an arctic environment, exhibiting a 2-4 year life cycle and reproduces at depth to maximize its time at the surface for feeding (Hirche, 1997; Falk-Petersen et al., 2009; Gislason, 2018). The ascending population, including eggs and nauplii, arrive at the surface in early spring and remain within the upper layers from May to July (Astthorsson and Gislason, 2003). During ascent, *C. hyperboreus* enters, either directly from the Iceland Sea or via advection from further upstream, the EIC, and is transported into the southwestern Norwegian Sea, from where it is further dispersed within the current systems in the Nordic Seas (Wiborg, 1955; Broms et al., 2009). The low abundance of young copepodite stages (CI-CIII) (Broms et al., 2009; Eilif Gaard, pers. comm.) suggests unsuccessful reproduction in the southern Norwegian Sea. Therefore, *C. hyperboreus* that occur in the southern Norwegian Sea most likely are advected southwards, from the Greenland and Iceland Seas.

### **1.2.3 Planktivorous fish stocks**

The Norwegian spring spawning herring is one of the largest herring stock in the world (Holst et al., 2002). The stock performs a clockwise migration throughout the season. After spawning along the Norwegian coast in spring, the herring has exhausted its food reserves and begin their feeding migration in the eastern Norwegian Sea and migrate westwards (Fig 1). In some years

the herring stock is observed along the western side along the JMF, while in other years the fish has crossed the front and entered the Iceland Sea. Further into the migration season the stock is commonly aggregated east of Iceland (í Homrun, et al., in prep). When feeding intensity decreases in late summer (Holst et al., 2004), the stock migrates towards their overwintering area, which since the 1990s has been located off the coast and in fjords west of northern Norway (Kvamme et al., 2003). Here they remain until the southward spawning starts the following year.

Herring has preferred prey species and prey size that reflects their energy content. *C. finmarchicus* in late copepodite stages and *C. hyperboreus* is amongst their favourite food, while *Metridia* spp., krill and amphipods are eaten in some productive areas at certain times (Dalpadado et al., 2000; Gislason and Astthorsson, 2002; Melle et al., 2020).

It has been hypothesized that herring adapts their feeding migrations according to the seasonal timing in production and distribution of *C. finmarchicus*. Consequently, the herring performs an east to west migration from lower to higher densities of overwintering *C. finmarchicus* individuals during the feeding season (e.g. Pavshikov, 1956; Østvedt, 1965; Broms et al., 2012; Melle et al., 2020). The larger and more nutritious, *C. hyperboreus*, is increasingly preyed upon further westwards during the migration (Dalpadado et al., 2000; Melle et al., 2020). Arriving to the frontal region, i.e. the JMF, the herring waits for the surface layer above the thermocline to become sufficiently warm to continue its migration across the front and into the Iceland Sea (Jakobsson and Østvedt, 1996; Misund et al., 1997).

### 1.3 Previously discussed shifts

Changes in the marine climate may influence the herring stock directly e.g. in terms of a temperature change or indirectly via a change in prey composition and availability (Holst et al., 2004). Hydrographic changes caused by advection can usually be predicted from upstream hydrographic properties along current branches with a time lag (Holliday et al., 2008; Mork et al., 2014). Both the Norwegian Sea and the upstream Iceland Sea have experienced notable shifts in the hydrographic conditions since the 1950s. These can be divided into two different prolonged periods, the warm years (1950-1964) and the cold years (1965-late 1960s/early 1970s).

The warm years were characterized by the westward migration of the large herring stock, feeding in the heated surface layer within the EIC in May and June, on their way to north Icelandic waters (Østvedt, 1965; Jakobsson and Østvedt, 1996). The change from warm to unusually cold conditions in the Iceland Sea occurred abruptly in the mid-1960s, with a temperature drop of 4°C within the EIC. The anomalously high air pressure over Greenland during the cold years lead to increased influx of polar water from the East Greenland Current, and combined with decreased Atlantic water inflow from to the North Icelandic shelf, turned the EIC from an ice-free arctic current into a wider, ice-drift polar current (Malmberg, 1969; Malmberg and Valdimarsson, 2003), pushing the JMF further eastwards (Blindheim et al., 2000)



and creating colder conditions within the Norwegian Sea (Malmberg et al., 1966). As northerly winds gradually weakened in the late 1960s, coinciding with an increasing NAO index, the Norwegian Sea freshened (Blindheim et al., 2000; Mork et al., 2014). The reduced transport of Atlantic water to the waters north of Iceland lead to stronger stratification, and thus decreased mixing and renewal of nutrients, which ultimately resulted in reduced phytoplankton and zooplankton production (Thórdardóttir, 1977). Nevertheless, the zooplankton biomass within the EIC off the northeast Icelandic coast remained relative unchanged as the local production of *C. finmarchicus* decreased, the increased influx of the East Greenland Current resulted in increased numbers of *C. hyperboreus* (Astthorsson et al., 1983; Astthorsson and Gislason, 1995) which were subsequently widely dispersed within the eastern Norwegian Sea (Malmberg et al., 1966). During the warm years, the herring was observed to cross the JMF, but during the cold years the herring was observed to migrate along the JMF at a more easterly position and did not enter the EIC due to the absence of a heated surface layer above the thermocline (Jakobsson and Østvedt, 1996; Holst et al., 2002).

#### 1.4 Motivation of the study

Since the early 1990s, the Faroe Marine Research Institute (FAMRI) has established six standard monitoring sections, radiating out from the Faroe Islands. Section N, which is the focus of this thesis, protrudes northwards into the southwestern Norwegian Sea, cutting through MNAW, crossing the IFF, and into subarctic waters comprised of the MEIW and NNAW as well as the underlying deeper waters (Fig.3). The aim of establishing the biological monitoring program at Section N was to focus on the state of the pelagic ecosystem by regular collecting hydrographic and zooplankton data. After the post-2003 expansion of the pelagic stocks within the southwestern Norwegian Sea, and the overall reduction in zooplankton biomass within the Norwegian Sea, further understanding of the zooplankton community structure was warranted (ICES, 2018).

Contrasting conditions characterize the waters east of Iceland and within the Atlantic waters inflow during the mid to late 1990s. While unusual cold conditions prevailed in 1996-1998, referred to as the Polar Years, in the Iceland Sea (Malmberg and Valdimarsson, 2003), the weakening of the SPG (Hátún et al., 2005) lead to gradual warming of the Norwegian Sea (Holliday et al., 2008). In 2003, a so-called ‘Atlantification’ propagated throughout the Nordic Seas (see Section 1.1.3), but the conditions reversed around 2015. Between 2013-2015, unusually deep convection occurred within the subpolar North Atlantic, causing the largest drop in seawater salinities ever observed in the northeast Atlantic (Holliday et al., 2020). This event resulted in an inflated SPG, an accelerating circulation of the NSG, yet, again, a tendency toward more ‘Arctic conditions’ within and around the Norwegian Sea (ICES, 2020; Skagseth et al., in prep).

Understanding the impact of these major oceanographic changes on the *Calanus* community and thus the prey availability for the herring stock since the 1990s is the essence of this thesis. I relay on the existing research presented in the book “The Norwegian Sea Ecosystem” (Skjoldal et al., 2004) and update this discussion primarily on the backdrop of the ‘Atlantification’ around 2003, complemented by aspects of the post-2015 shift.

## 1.5 Objective

The objectives of this study were as follows:

- to introduce a time-series for *C. finmarchicus* and *C. hyperboreus* at Section N and link the interannual variability in abundance and composition to phytoplankton dynamics and hydrography (Paper I)
- to investigate a ‘MEIW and *Calanus* spp. transport hypothesis’ by putting the interannual changes of the *Calanus* spp. time series, within the subarctic region at Section N, in a larger scale perspective, and to include zooplankton observations and influx of MEIW from the Iceland Sea (Paper II)
- to explore seasonal abundance and stage development of *C. finmarchicus*, combined with vertical distribution, reproduction, feeding activity and lipid content north and south of the IFF in order to improve our understanding of the biological mechanisms in different hydrological environments (Paper III)
- to investigate prey availability, prey selection and stomach fullness during contrasting hydrographic periods and relate this information to the herring distribution since 1996 (Paper IV)
- to explore the hypothesis that the increased abundance of calanoid copepods in the near-surface layer during spring increases the motivation for vertical migration of pelagic and mesopelagic species, which therefore can explain the increased diel vertical migration activity during the season (Paper V)

## 2 Materials

In addition to own field research, various datasets were used in order to achieve the objectives and are listed below. The data used in Paper V is not included here.

*FAMRI*: Hydrographic properties (temperature and salinity), measured down to 1300 m depth, and accompanying vertical zooplankton WP-2 net hauls from 50 m depth to the surface. A fluorometer mounted on the CTD (Conductivity, Temperature, Depth) provided concurrent fluorescence profiles. The hydrographic properties were measured up to four times a year from 1988 to 2020 and zooplankton monitoring occurred twice a year, in May and late August/early September, since 1993 to present.

*GlobColour Project*: Satellite based chlorophyll *a* data, used to estimate bloom initiation, were downloaded from <http://www.globcolour.info>, covering the years 1998 to 2014.

*NANSHY (North Atlantic and Nordic Seas hydrography) database*: Compilation of CTD profiles, collected by numerous organizations in the North East Atlantic (Nielsen, 2016).

*IESNS data*: From this database, termed PGNAPES (Planning Group for Northeast Atlantic Pelagic Ecosystem Surveys), we used zooplankton biomass, collected in May, in the Norwegian and Iceland Seas, from 1996 to 2020 (WGINOR, 2018).

*Gyre index (1993-2011)*: The gyre index represents the strength of the cyclonic SPG circulation in the North Atlantic and the properties of the Atlantic water entering the Nordic Seas (Hátún et al., 2005). It is based on measurements of sea surface height from AVISO (Larsen et al., 2012; Hátún and Chafik, 2018).

*Drifters*: Testing for near-surface advection, surface drifters passing through the EIC and towards Section N, were downloaded from the NOAA AOML website (<http://www.aoml>), covering the years from 1991 to 2016.

*Satellite sea surface temperature*: Daily sea surface temperatures from satellite observations in May 2020 for the Norwegian Sea region were downloaded from <http://marine.copernicus.eu>.

*Herring diet composition*: Stomach content, collected during the IESNS survey in May, from 2007-2011 and 2017-2020 were utilized. Accompanying this dataset are fish length and weight.

### 3 Results and Discussion

Papers I and Paper III describe the *Calanus* community, with a particular emphasis on the subarctic region after the Atlantification in 2003, which Paper II supplements with detailed hydrographic information. Paper IV provides new results on the post-2015 shift back to more subarctic conditions. Paper V supplements Paper IV with information on vertical migration of herring that are known to dip into a so-called ‘cold fridge’ to feed on *Calanus* spp.

#### 3.1 Habitat and population structure across the IFF

In this thesis work, it was documented that the IFF acts as a barrier between the southern and northern area at Section N (Fig. 3b), allowing minimal exchange of copepods across the frontal region (Paper I, Paper II). Therefore, the zooplankton population, south and north of the IFF, can largely be considered as two separate populations.

The living conditions along Section N provide different habitats, both in terms of advection patterns (Paper II), temperature conditions and spring bloom onset (Paper I, Paper III). This is evident by the (i) notable difference in *C. finmarchicus* female sizes, being significant larger within the subarctic region than in the Atlantic region (Fig. 5; Paper III). This is also confirmed by observations in the near vicinity of Section N by Jónasdóttir et al. (2008), (ii) distinct *C. finmarchicus* stage composition observed in Atlantic water and subarctic water, from 1993 to 2003, during the annual May survey (Fig. 6), and (iii) significant difference in abundance of *C. hyperboreus* between the regions (Fig. 7).

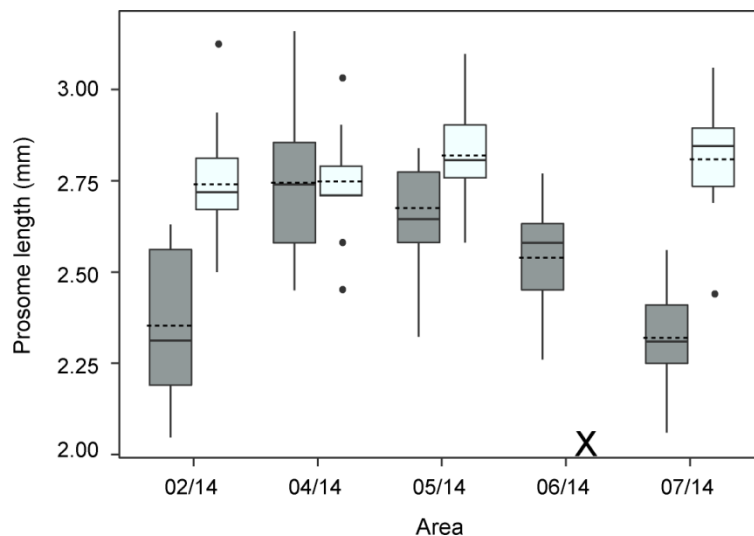


Fig. 5. Seasonal variation in female prosome length in Atlantic water (grey box) and subarctic waters (white box) within the upper 50 m at Section N. The vertical lines show standard error. The solid and dotted horizontal lines represent the median and mean values. The black cross indicates that less than 10 females were found and measured.

### 3.2 Changes in *Calanus* spp.

#### 3.2.1 Interannual variations in *Calanus finmarchicus* stage composition in spring

The zooplankton time series at Section N (Fig. 6) covers 28 years of observations in May (Paper I). This work could identify several different patterns based on this unique observation period. The time-series provides essential information on the available food resource for pelagic fish. The sampling years prior to 2003 showed that the abundance of *C. finmarchicus* within the warmer Atlantic water, south of the IFF, was always dominated by the small and newly produced individuals, i.e. stage CI-CIII, while the numbers of the larger and older individuals from the overwintering generation ( $G_0$ , stages CIV-CVI) were significantly lower (Fig. 6b). In contrast, within the colder subarctic waters north of the IFF, the stage composition was dominated by the older stages whilst the younger stages were in very low abundance (Fig. 6a). Thus, the difference in stage composition shows that prior to 2003, the reproduction has started earlier in the Atlantic water than in the subarctic water. In 2003, the stage composition, and thus the timing of reproduction at the subarctic part of Section N in May, suddenly changed (Fig. 6a and 6c) and became identical to the timing south of the IFF (Fig. 6b and 6d).

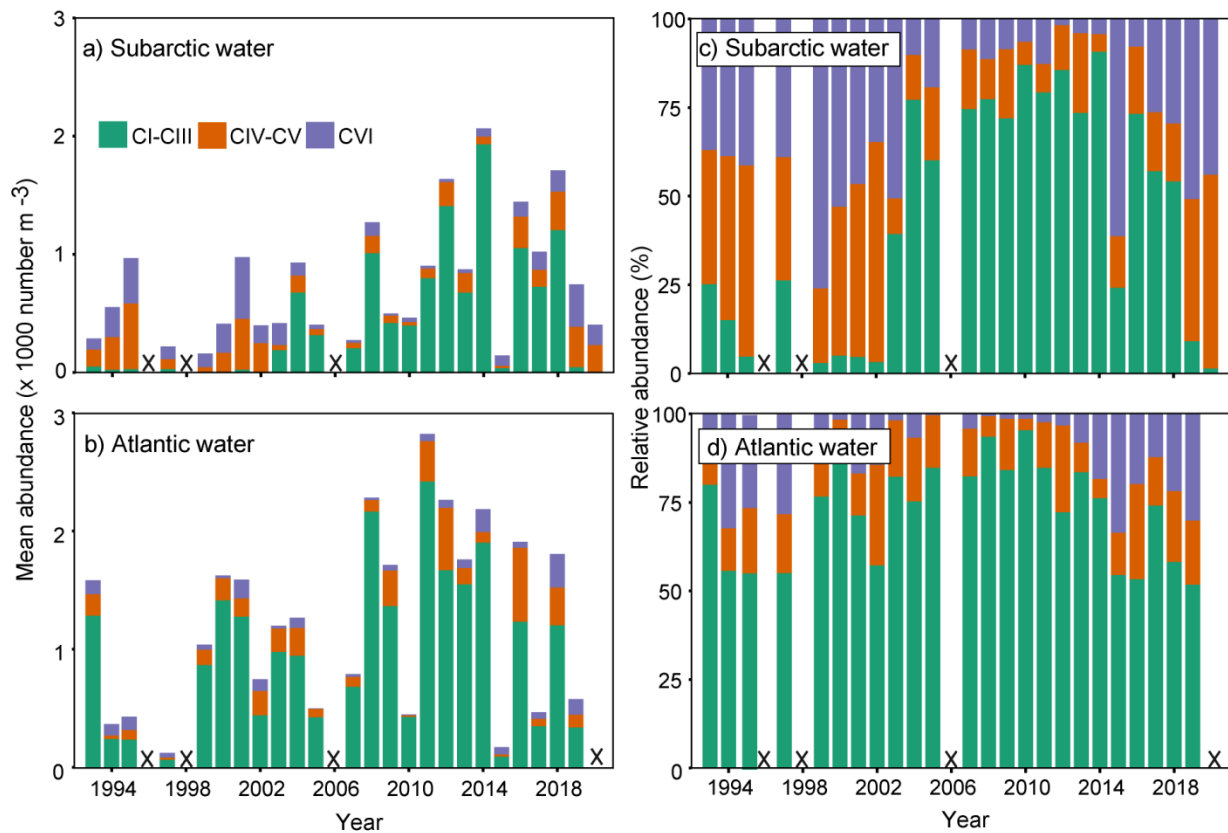


Fig. 6. Interannual variations in the mean abundance (numbers  $m^{-3}$ ) and relative abundance of *C. finmarchicus* developmental stages in May, in Atlantic water (bottom) and subarctic water (top) at Section N. Mean abundance and relative abundance are displayed in the left panels (a and b) and right (c and d), respectively. Years with missing data are indicated by crosses.

### 3.2.2 Interannual abundance of *Calanus hyperboreus*

A sudden reduction in the abundance of *C. hyperboreus* coincided with the phenological shift of *C. finmarchicus*, north of IFF (Fig. 7, Paper I, Paper II). Prior to 2003, *C. hyperboreus* used to be common in the zooplankton community, particularly in the subarctic waters with an abundance approximately 10 times higher compared to the Atlantic water. However, *C. hyperboreus* largely disappeared from Section N after 2003.

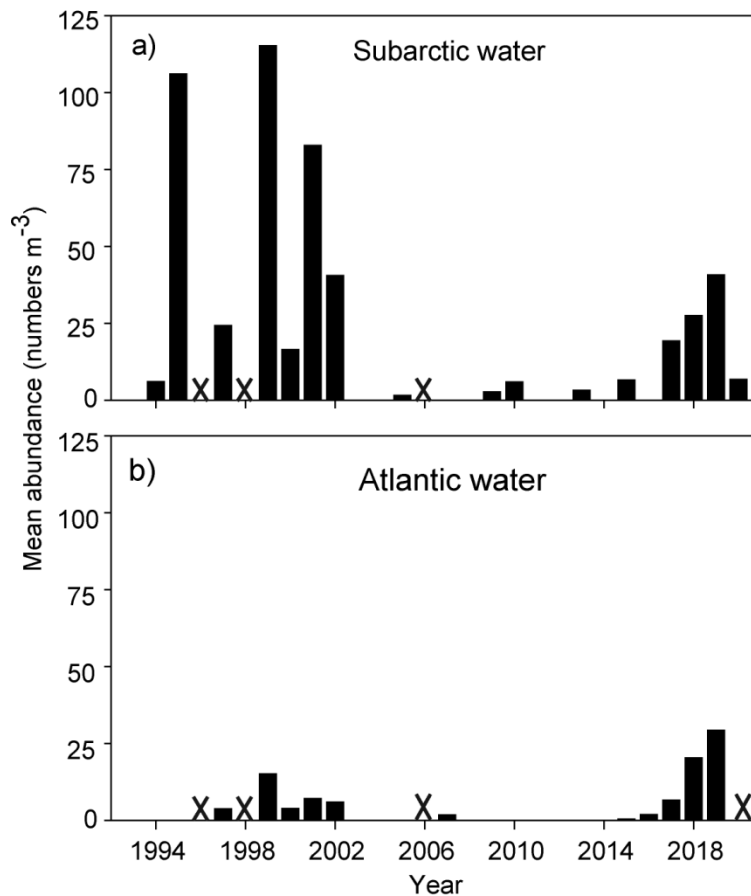


Fig. 7. Mean abundance of *C. hyperboreus* in the (a) subarctic water and (b) Atlantic water in May from 1993 to 2020. Years with missing data are indicated by crosses.

## 3.3 Potential factors influencing the 2003 shift

### 3.3.1 Phytoplankton bloom – phenology and intensity

Different timing of *C. finmarchicus* reproduction in the subarctic waters compared to the Atlantic water prior to 2003 cannot be explained by the variable primary production – both in timing and biomass – in these two water masses.

The main period of egg production and growth of *C. finmarchicus* is tuned to the spring bloom (e.g. Niehoff et al., 1999; Stenevik et al., 2007), while the developmental rates of copepodite stages are temperature dependent (Miller and Tande, 1993). The near-surface temperatures along Section N in May is  $\sim 8^{\circ}\text{C}$  in the Atlantic water and  $\sim 4^{\circ}\text{C}$  in the subarctic water at (Paper I, Paper III). This temperature difference places a restriction on the developmental rates north of the IFF as the stage duration from spawning to CI can be estimated to be three and four weeks in the Atlantic and subarctic waters, respectively (Campbell *et al.*, 2001). Thus, CI-CIII in May (Fig. 6) are spawned around mid April within the northern region and around late April in the Atlantic water.

Surface chlorophyll *a* from satellite observations, covering Section N and the surrounding area showed that the spring bloom typically starts around late April, north of the IFF, and in early June, south of the IFF (Fig. 8a, Paper I). This means that spawning roughly coincides with the bloom in the northern region, while there is a four week mismatch between spawning and bloom onset in the south (Paper I, Paper III). The bloom initiation can, however, vary three to five weeks in each respective domain (Fig. 8b), which will modulate the match-mismatch between the years.

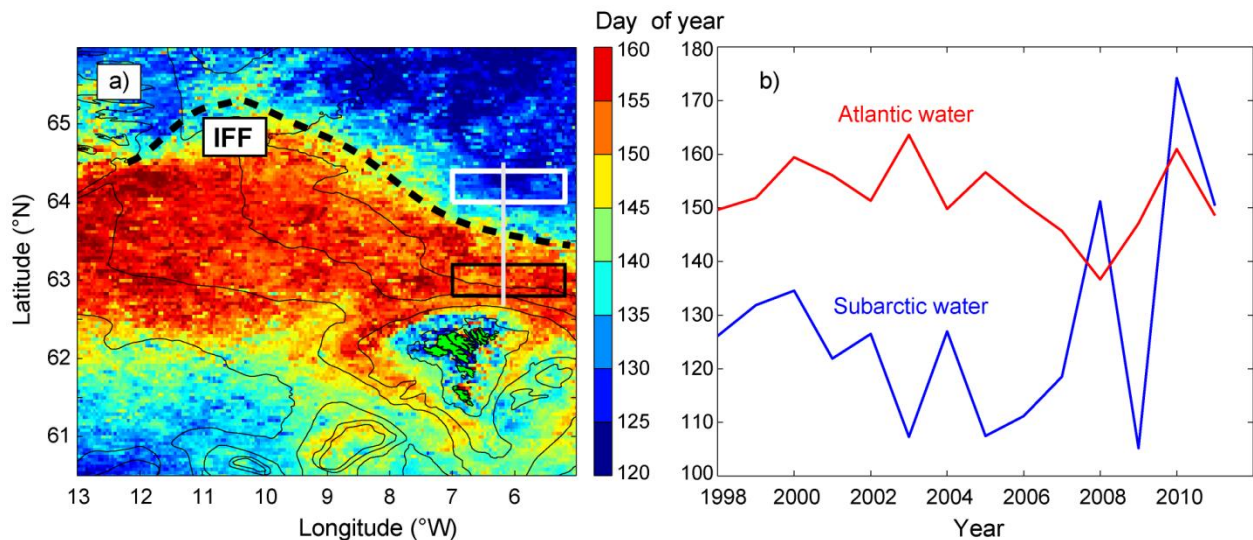


Fig. 8. Onset of the spring bloom from 1998 to 2011. (a) Average time (day number) of the bloom initiation and (b) associated time-series of average day number of the bloom onset for each year in the Atlantic water (red) and subarctic water (blue). The values in (b) have been extracted from the boxes shown in (a). The dashed line illustrates the Iceland-Faroe Front (IFF).

In addition to the earlier increase in phytoplankton biomass, the mean concentrations within the upper 100 m tended to be higher within the northern region in May, with the exception of a few random years (Fig. 9 in Paper I). No correlation was observed between the phytoplankton trends and the phenological shift. Thus, primary production was not the main driving mechanism behind the shift in stage composition of *C. finmarchicus*.

### 3.3.2 Not warming per se

Since the mid-1990s the temperature and salinity have gradually been increasing within the Nordic Seas, reaching a sharp peak in 2003 (Fig. 9; Malmberg and Valdimarsson, 2003; Larsen et al., 2012; Skagseth and Mork, 2012; Holliday et al., 2020).

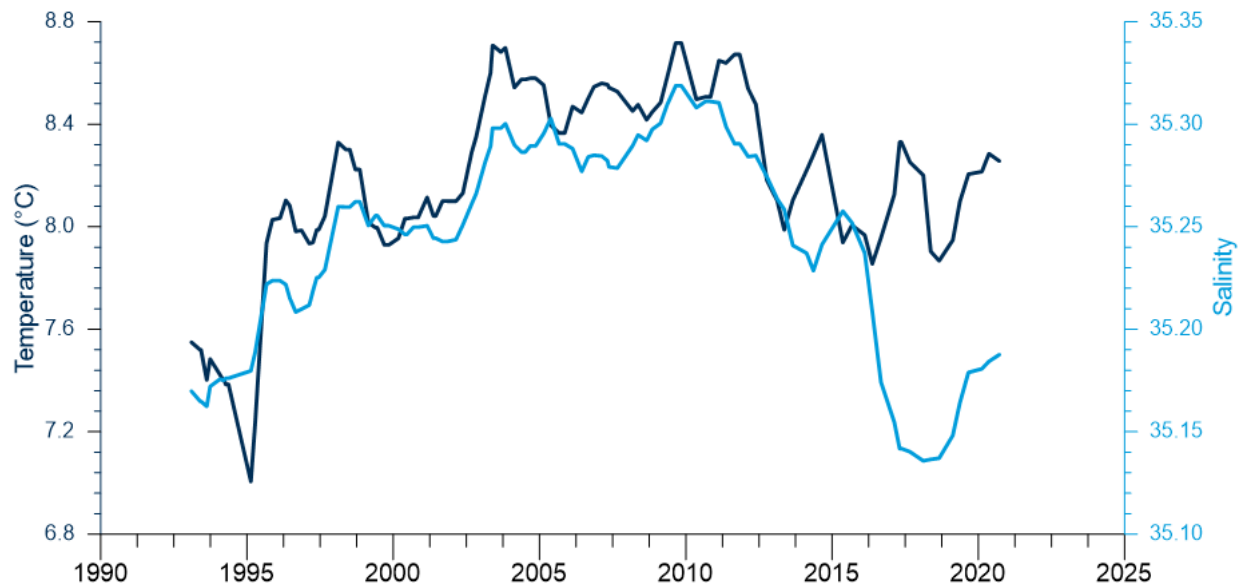


Fig. 9. Temperature and salinity variations in Atlantic water at Section N. The temperature (black) and salinity (blue) are averaged over a 50-m depth layer and show a 1-year running mean of deseasoned values. Updated from Larsen et al. (2012).

The temperature time series in the northern region at Section N also showed a marked temperature increase of around 1°C around 2003, which peaked the following year. However, a temperature increase by 0.5-1°C is only expected to shorten the developmental rates in the subarctic water by 3-6 days (Campbell et al., 2001). Thus, despite the sudden warming in 2003, faster developmental rates are not sufficient to support the hypothesis that temperature was a key mechanism behind the phenological change of *C. finmarchicus* in 2003.

A third possibility behind the shift in population dynamics, north of the IFF, which accounts both *C. finmarchicus* and the arctic expatriate, *C. hyperboreus*, could be related to a redistribution of water masses. This is discussed in the following sections.

### 3.3.3 Advection

The ecology of the southern region at Section N is largely influenced by the MNAW and the  $G_0$  *C. finmarchicus* individuals it contains (Paper III). On the other hand, the composition of the



water mass, north of the IFF (Fig. 3), suggest that this region is resupplied in spring with *C. hyperboreus* from the Iceland Sea while *C. finmarchicus* is supplied from both the Iceland Sea and Norwegian Sea (Paper II, Paper III). Recently Strand et al. (2020) has pointed out that the *C. finmarchicus* population within the Norwegian Sea produces two generations while only one generation is produced in the Iceland Sea.

The significantly higher abundance of *C. hyperboreus* north of the IFF (Fig. 7b), suggests that there is an association between the current system and the abundance of *C. hyperboreus* in the off-shore waters north and northeast of Iceland (Astthorsson and Gislason, 2003), hereafter collectively also referred to as the western region. The main pathway for *C. hyperboreus* reaching Section N is probably via advection by the intermediate depth MEIW layer (Helland-Hansen and Nansen, 1909; Wiborg, 1955). Considering *C. hyperboreus* as an indicator species of these upstream regions, it is plausible that the sudden co-occurring reduction in abundance of *C. hyperboreus* and the phenological shift of *C. finmarchicus*, north of IFF, was caused by a reduced eastward extension of these arctic waters into the southern Norwegian Sea, as described below.

#### *Reduced MEIW influx after 2002*

Monitoring hydrographic conditions in, or in close proximity to, frontal regions is challenging due to marked short term variability. The region around Section N at the southwestern border between the Iceland and Norwegian Sea is more sensitive to the variable eastward influx of EIW/MEIW into the southwestern Norwegian Sea than the rest of the Norwegian Sea (Paper II).

Two contrasting years, 2002 and 2003, are presented to illustrate the variable of the eastward extent of EIW/MEIW (Fig. 10). The eastward extent of EIW/MEIW was much reduced in 2003 (Fig. 10b) compared to 2002 (Fig. 10a), and it did not cross the subarctic region at Section N. In 2003, warm Atlantic water was more widespread in the region and the JMF was displaced further westwards than in 2002, indicating a decreased volume influx from the western upstream region.

The averaged (1992-2016) areal Temperature-Salinity (T-S) diagram shows the four water masses that comprise Section N (Fig. 11). We see that two of them, i.e. MNAW and NSAIW, are dominant mode waters with relative stable characteristics (Paper II). In contrast, the NNAW and MEIW are more spread out in T-S space due to rapid mixing with the surrounding larger water masses. Increased frequencies of NNAW T-S characteristics appear after 2003 while notable less is recorded in the T-S range of MEIW. This suggests that the increase of NNAW T-S space has largely replaced the T-S space for MEIW, which flow along similar isopycnals.

Using the T-S criteria by Read and Pollard (1992), we extracted a time series to represent the volume of MEIW at Section N (Fig. 12). The MEIW covered a large cross-sectional area from the mid-1990s to early 2000s, followed by a sharp decline in 2003, with the unsmoothed value showing that the MEIW became virtually absent that year. This supports our deduction of a decreased volume influx from the western upstream region in 2003.

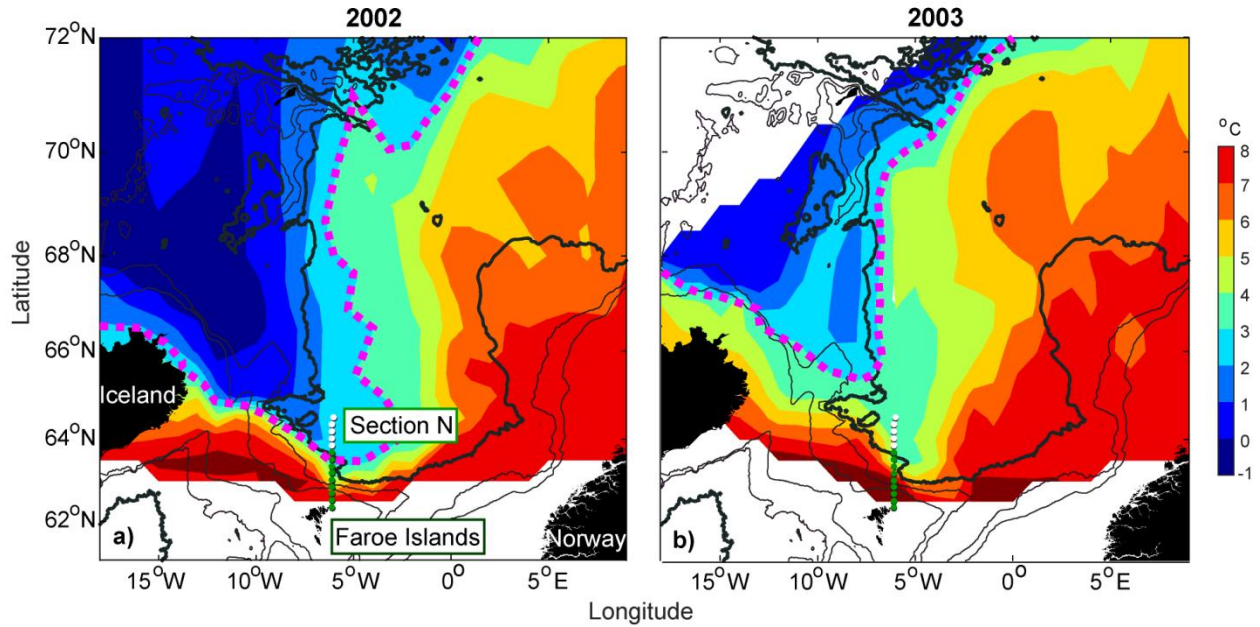


Fig. 10. The eastward extent of the EIW/MEIW tongue at 100m depth in May (a) 2002 and (b) 2003. The subarctic region along Section N is the northernmost stations shown in white. The eastward extension of the subarctic water at 3°C is highlighted with the dashed pink curves. The 500, 1000 and 2000 (bold) m isobaths are also shown.

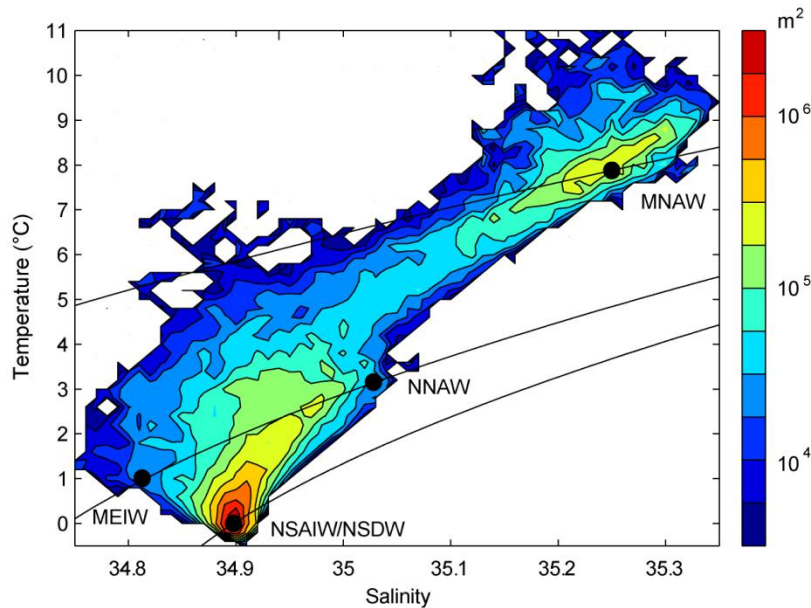


Fig. 11. An areal T-S diagram of water masses at Section N, showing the average over the period 1992–2016. The values in the T-S diagram are square meters and represented by salinity and temperature intervals of 0.02 and 0.2 °C, respectively. Core areas (T-S ranges definitions) for the water masses are indicated with black dots. The black lines represent three selected values of potential density ( $\sigma_\theta$ ). See Table 1 for abbreviations.

### Association between MEIW and *Calanus spp.*

Positive association is observed between the variable volume of MEIW at Section N and abundance of *C. hyperboreus*, north of the IFF (Fig. 12a, Paper II). Sharp peaks in MEIW in 1994, 1998 and 2001 are followed by increased peaks in *C. hyperboreus* one year later. After the drop in 2003, smaller fluctuations in MEIW coincided with a moderate appearance of *C. hyperboreus*. Thus, the years before and after 2003 can be defined as high and low influx periods, respectively. Similar variations in arctic water from the Iceland Sea and *C. hyperboreus* are also observed at the Svinøy section in the eastern Norwegian Sea (Skagseth, et al., in prep). This stipulates the importance of the eastward extent of EIW/MEIW (e.g Wiborg, 1955; Østvedt, 1965) and confirms that *C. hyperboreus* can be used as a biological tracer for these subarctic waters from the western region.

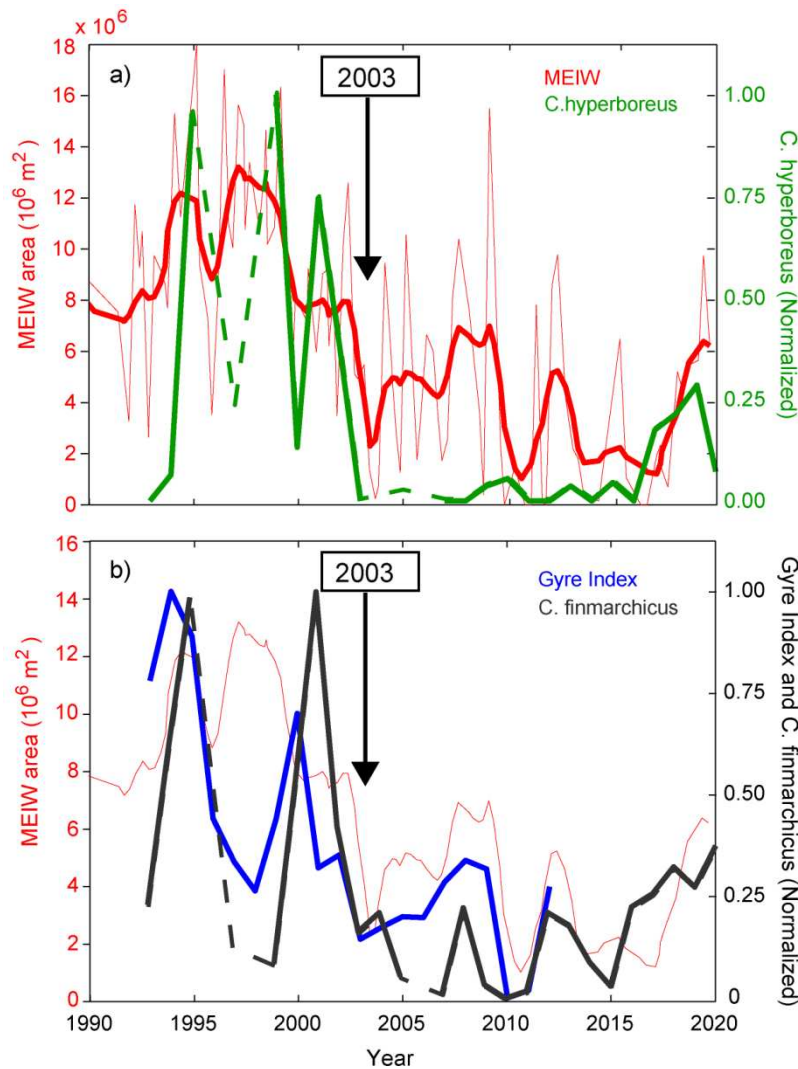


Fig. 12. Cross-sectional area of MEIW at Section N and mean abundance of *Calanus* spp. within the subarctic region at Section N in May. a) Mean abundance of *C. hyperboreus* (green) and the MEIW area

(red) are shown. The thin red line represents unsmoothed values from individual occupations of this section, while the thick red line shows the smoothed low-pass filtered MEIW trend (filter width of four data points). In (b), the mean abundance of large *C. finmarchicus* (stage CIV-CVI, black) and the gyre index (blue) presented by Larsen et al. (2012) has been plotted. No zooplankton data are available in 1996, 1998 and 2006, which is indicated by the stippled connecting lines.

As *C. finmarchicus* is endemic to both the Iceland Sea and the Norwegian Sea, it is more difficult to demonstrate a relationship between advection and stage composition. However, we suggest that the identical phenology along Section N since 2003 is due to decreased influx of subarctic waters and the  $G_0$  individuals it contains. This is replaced by an increased influence of NNAW, containing increased numbers of younger individuals, which is similar to the phenology pattern south of the IFF where Atlantic water dominates (Fig. 14; Paper I, Paper II).

The MEIW flows at intermediate depths while the deeper arctic intermediate water masses from the Iceland Sea are found at >500 m and are a part of the overflow that is advected into the Norwegian Sea (Serra et al., 2010; de Jong et al., 2018; Semper et al., 2020). This is the overwintering depths for both *Calanus* spp. in the Iceland Sea (Gislason, 2018) and it is therefore likely that individuals recorded at Section N are also advected with this water mass. This remains to be investigated.

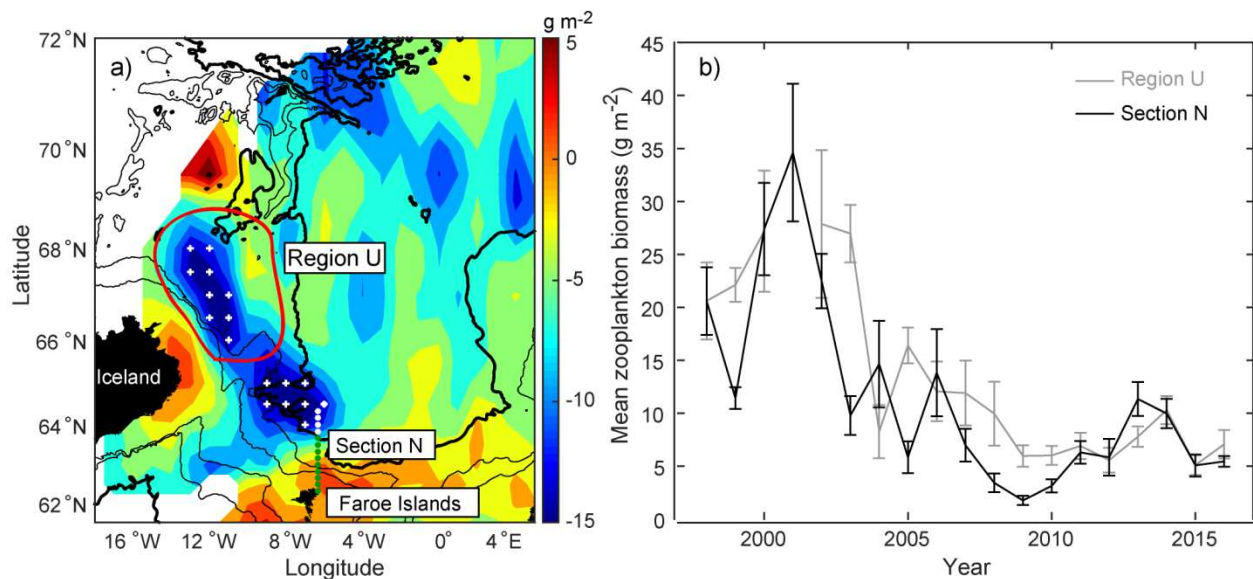


Fig 13. Zooplankton biomass from the IESNS survey in May. a) The difference in zooplankton biomass before 2003 (1998–2002) versus after (2003–2016) (later years – early years). b) Spatially averaged zooplankton biomass in May from 1998 to 2016 in Region U (grey) and the region representing Section N (black), together with their 95% confidence intervals (vertical lines). The geographic location of these regions is shown in (a). The upstream Region U and the downstream region, which the subarctic region along Section N (white dots) represents, were selected for time series analysis (white crosses) in (b). The 500, 1000 and 2000 (bold) m isobaths are shown.

*Post-2015 shift*

From 2015 to 2018 a gradual increasing abundance of the larger *C. finmarchicus* stages have been appearing with the subarctic water, north of the IFF (Fig. 6a and 6c, Paper IV). In 2019 and 2020, this transition has been identical to the composition prior to 2002. Similarly, the abundance of *C. hyperboreus* has also been increasing since 2015 (Fig. 7a). The increased abundance of *C. hyperboreus* and overwintered *C. finmarchicus* can also be linked to an increased area of MEIW at Section N (Fig. 12).

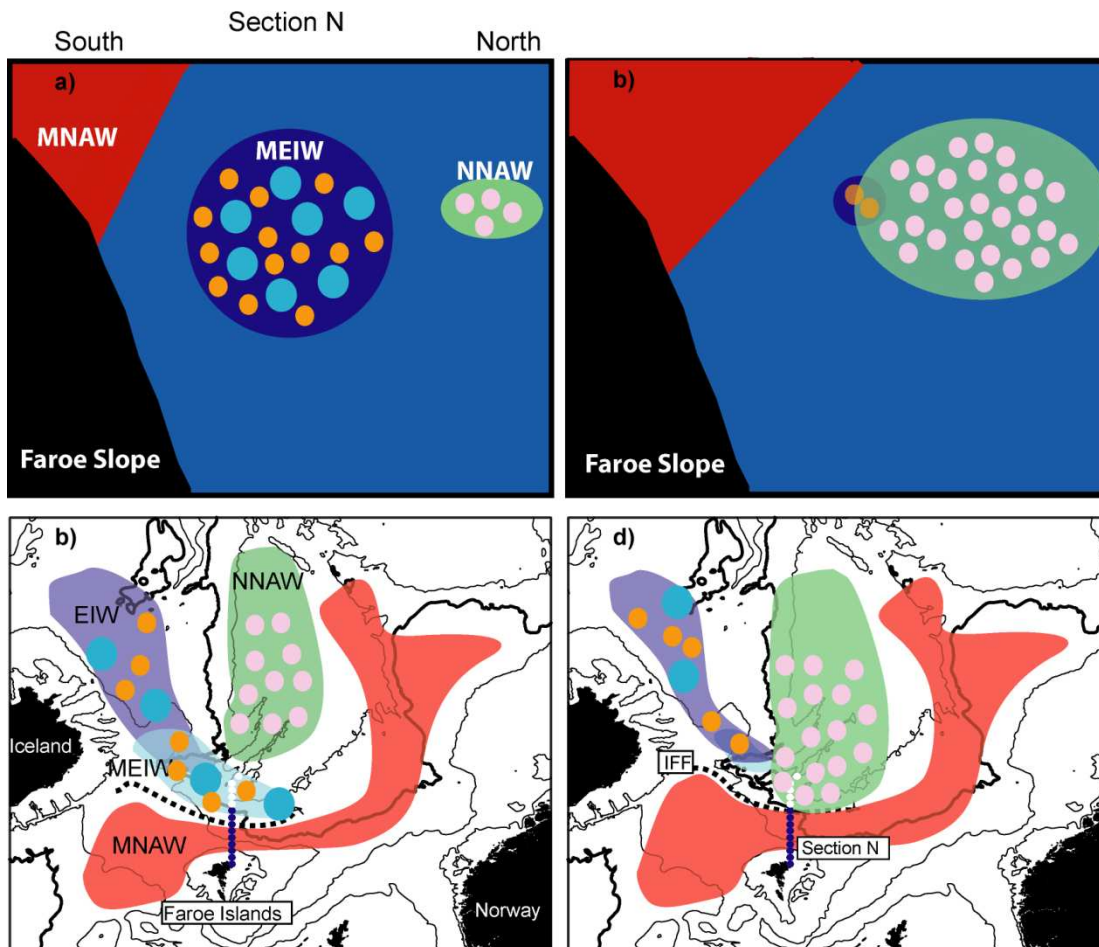


Fig. 14. A schematic sketch illustrating the contrasting conditions during (a) high EIW/MEIW influx and (b) low EIW/MEIW influx. The dots represent the population of *C. hyperboreus* (blue) and *C. finmarchicus* (orange) in the Iceland Sea and *C. finmarchicus* population (pink) in the Norwegian Sea.

### 3.4 Seasonal cycles of *C. finmarchicus*

The presence of a G<sub>2</sub> in August/September, north of the IFF, also appears to be dependent upon the eastward extent of EIW/MEIW (Paper I, Paper II). Paper I demonstrated that during the phenology shift, initiated in 2003, resulted in an increased numbers of young stages in late August/early September (hereafter simply September). These years can be defined as years with less EIW/MEIW influence (Fig. 12). In contrast, in September 1993 (Gaard, 1996) and 1995 (Paper I), which can be defined as years with increased EIW/MEIW influence, the subarctic region at Section N was dominated by the older stages from the G<sub>1</sub>.

Gonad development of *C. finmarchicus* females at Section N, in May, has shown to be more advanced in the Atlantic water than in subarctic waters (Gaard, 2002). This matches with the earlier onset of reproduction in the MNAW, south of the Iceland Faroe Ridge (Jónasdóttir et al., 2008), which transports individuals to the southern region at Section N. Additionally, it also agrees to the later onset of reproduction in the Iceland Sea (Gislason, 2018). The results from Paper II suggest that during the years with decreased EIW/MEIW influence, the EIW/MEIW component becomes replaced by the NNAW. This results in two production cycles of *C. finmarchicus* (Fig. 14; Strand et al., 2020) and thus becomes similar to the classical pattern south of IFF.

The dynamics between EIW/MEIW and NNAW components within the southwestern Norwegian Sea therefore appear to affect the *C. finmarchicus* phenology pattern later in the season with an increased abundance of younger and smaller stages and with a reduction in abundance of the older and larger stages. This, in turn, influences the food availability, quality and quantity, for the pelagic stocks.

#### 3.4.1 Fecundity and related factors

From July 2013 to July 2014, a seasonal study was conducted within the Atlantic and subarctic regions at Section N (Paper III). This period was characterized by a (i) similar pattern in stage composition of *C. finmarchicus* north and south of the IFF (Paper I), (ii) decelerated anticlockwise circulation within the Iceland Sea (de Jong et al., 2018) and in the Norwegian Sea (Skagseth et al., in prep). Although a similar phenology in stage composition prevailed, the populations in the two regions inhabit different environments (Fig. 2). Paper III showed that the feeding conditions improved four weeks earlier in the northern region compared to the southern region. The females, north of the IFF, were larger (Fig. 5) which promotes larger clutch sizes (Jónasdóttir et al., 2008; Head et al., 2013). Additionally, the northern females appeared to contain higher wax ester content when arriving to the surface layers in February. These advantages are reflected in the individual (Fig. 15e) and community egg production rates (Fig. 15g) that peaked in April, and coincided with increased abundance of young stages within the upper 50 m (Fig. 16c and 16d). These observations are in agreement with the studies by Heath et al. (2004b) and Jónasdóttir et al. (2008) who noted a similar pattern between individuals north and south of the Iceland Faroe Ridge.

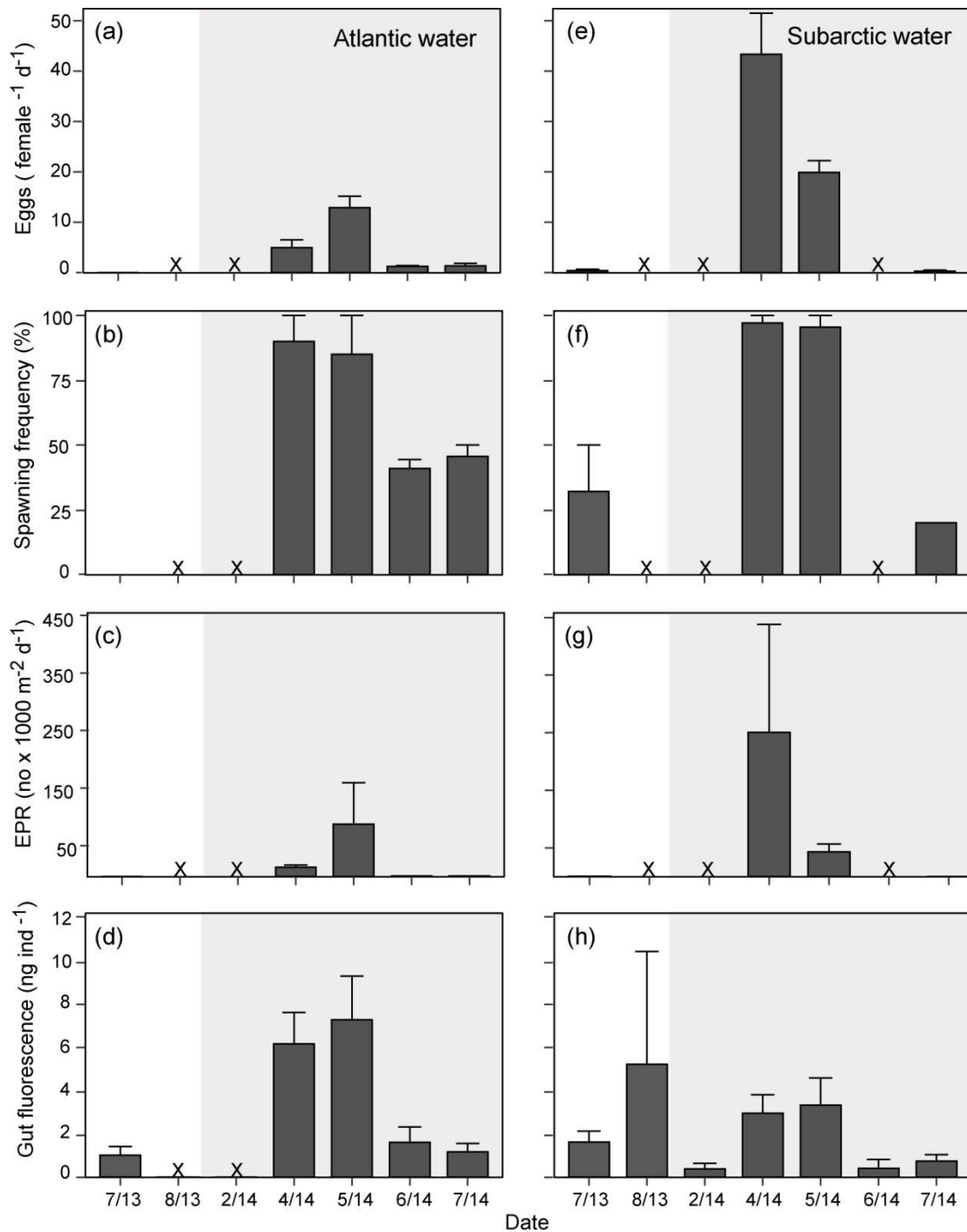


Fig. 15. Egg production rates (eggs female<sup>-1</sup> d<sup>-1</sup>), spawning frequency (% d<sup>-1</sup>), population egg production rates (eggs m<sup>-2</sup> d<sup>-1</sup> x 1000) and gut chlorophyll content (ng ind<sup>-1</sup>), as estimated by fluorescence, in *C. finmarchicus* females within the upper 50 m of the water column in Atlantic water and subarctic at Section N from July 2013 to July 2014. The vertical lines show standard error. The shaded area defines the reproductive period in 2014. Sampling dates where less than five females were caught are indicated by black crosses.

In the Atlantic water, we see low egg production rates in April and May that we cannot explain with the present data (Fig. 15a and 15c). Close to 50% of the  $G_0$  population had ascended to the surface layer in February (Paper III). This could be related to the lower wax ester content at depth, however further research is required to confirm this hypothesis. The relative early ascendance creates a mis-match to the bloom onset in late May/early June. Despite low food availability, the southern females showed nearly twice as much gut content concentration (Fig. 15d) compared to the northern females (Fig. 15h). Therefore, it can be speculated whether food quality suppresses the egg production rates in the Atlantic water rather than the decoupling between ascent and initiation of the spring bloom. From April to May the number of females increases by nearly a two-fold. These had a spawning frequency  $> 80\%$ , suggesting that most females had mature gonads and therefore had the potential to contribute to the population growth. Nevertheless, the egg production rates only slightly increased during this period.

When the onset of the spring bloom occurred in late May to early June in Atlantic water, the number of females in early June had already declined by nearly 90% which can largely be attributed to high mortality after prolonged spawning (Diel and Tande, 1992). The decline may also be partially attributed to predation pressure by e.g. herring that arrive to this area in May (Holst et al., 2004; Eliassen et al., in prep) to feed on the larger copepodite stages (Dalpadado et al., 2000; Gislason and Astthorsson, 2002, Paper IV).

In June and July, a portion of females, especially north of the IFF, are accumulating fat rather than investing the energy to egg production eggs (Paper III). The wax ester accumulation coincides with the initiation of descent from the surface layers to overwintering depths, suggesting that wax ester fullness be a trigger for descent. The overwintering stock was mainly comprised by stage CV but a small fraction of the stock was represented by females in both regions. These stages had similar wax ester content at depth, which suggests that these females will be immediately ready to contribute to the reproduction the following spring.



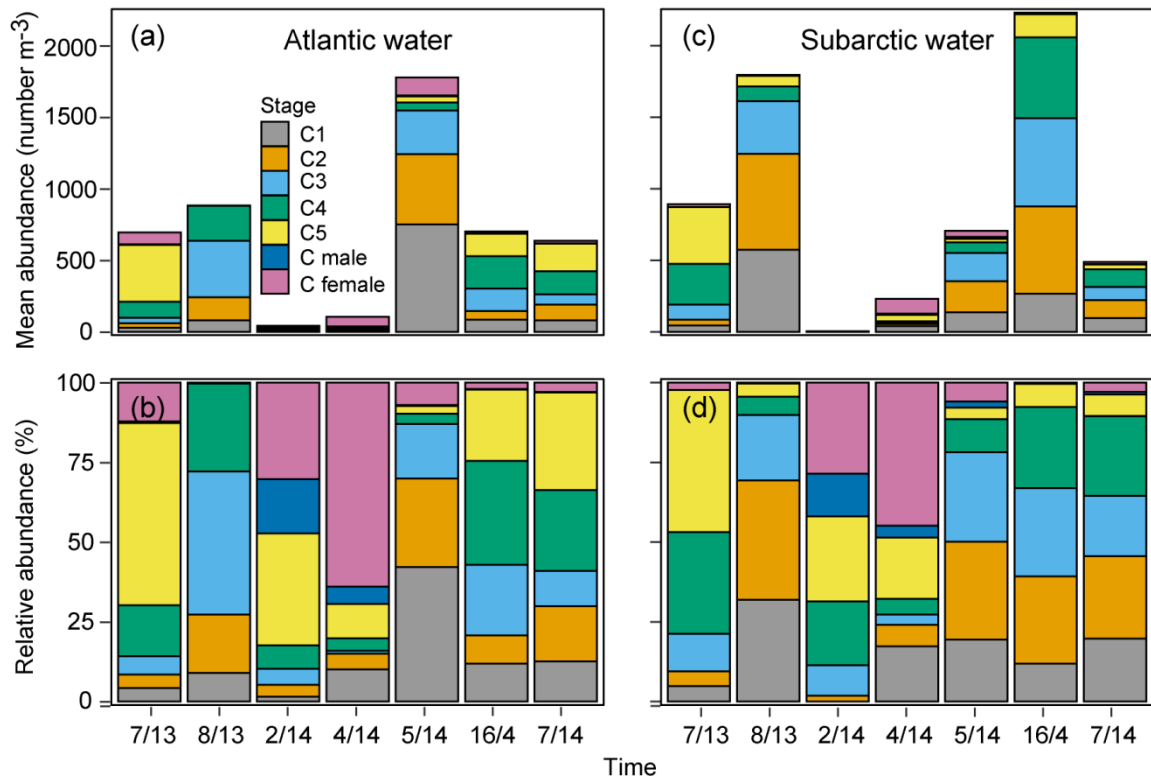


Fig. 16. Seasonal variation of *C. finmarchicus* in abundance (numbers m<sup>-3</sup>) within the upper 50 m in Atlantic water (south) and subarctic waters (north) at Section N.

### 3.5 Consequences for herring

#### 3.5.1 Dial vertical migration

Based on acoustic data, increased amounts of herring, as well as blue whiting, are recorded at Section N from May to December that comes to the region to feed near frontal areas (Paper V). During day-time herring is observed at around 200-300 m depth, although some remain within the surface layers both day and night. Zooplankton were too small to give a direct acoustic signals, however other studies have shown that herring are found at these depths, likely searching for larger prey (Nøttestad et al., 2007; Melle et al., 2020).

#### 3.5.2 Diet intake

Soon after the Atlantification in 2003, and the coinciding drop in zooplankton biomass concentrations over the Norwegian Sea, the herring has been aggregating in the southwestern Norwegian Sea in May to feed (ICES, 2020; Eliassen et al., in prep). In 2020, the core of this western feeding area was located within the subarctic waters immediately north/west of the junction between the IFF and the JMF. This area was characterized by the highest zooplankton

biomass (Fig. 17) that was mainly represented by overwintered stages and the derived adult stages of *C. finmarchicus* and *C. hyperboreus*, which was also reflected in their diet (Paper IV).

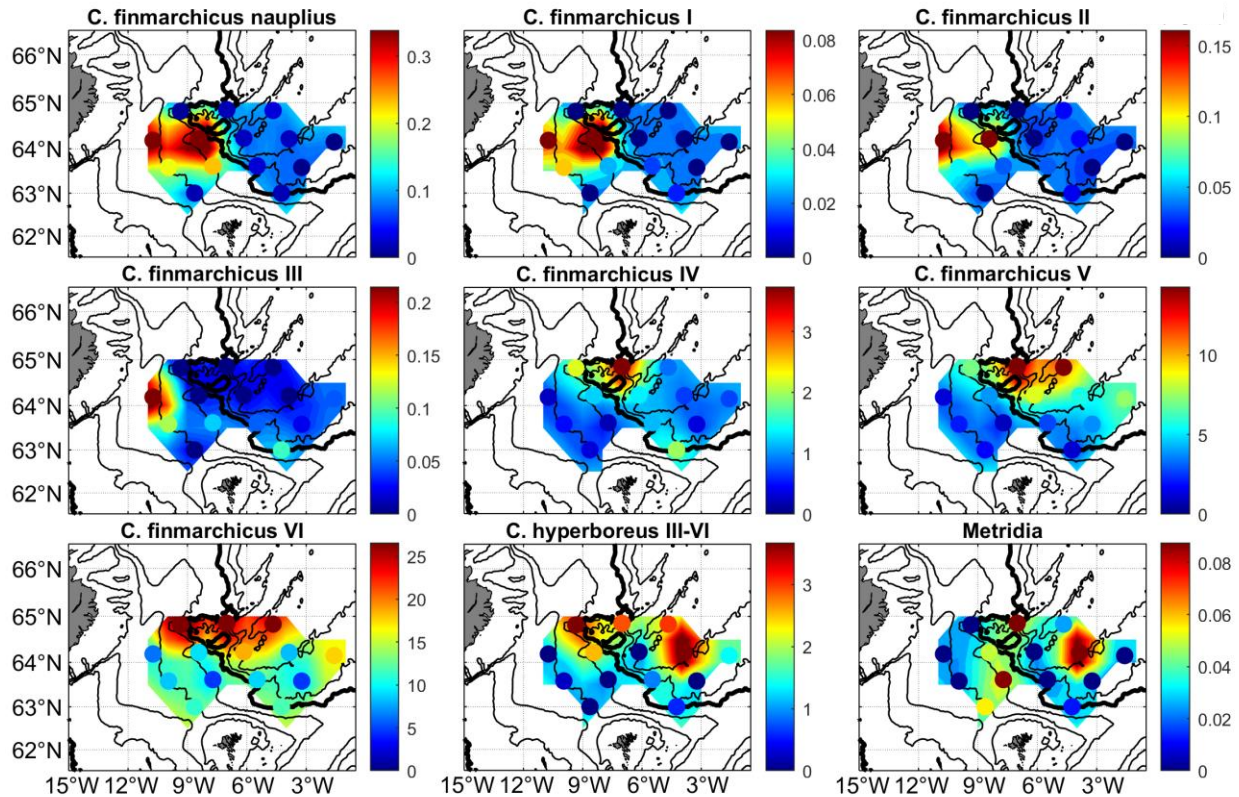


Fig. 17. Relative biomass of *C. finmarchicus* developmental stages, *C. hyperboreus* and *Metridia* spp. in May 2020. The dots represent the sampling positions. The 200, 500, 1000, 2000 (bold) and 3000 m depth contours are shown. Note that the scales vary.

Apart from the east to west increase in diet intake, we identified a notable difference in the stomach fullness index during the periods 2007-2011 and 2017-2020 (Fig. 18). The earlier period, which is characterized with weak MEIW influx, showed a lower stomach fullness index compared with the later period that is under greater influence of MEIW influx. This suggests that the food availability for herring in May is highly dependent upon the variable eastward intrusion of the arctic waters from the western region (Paper II, Paper IV).

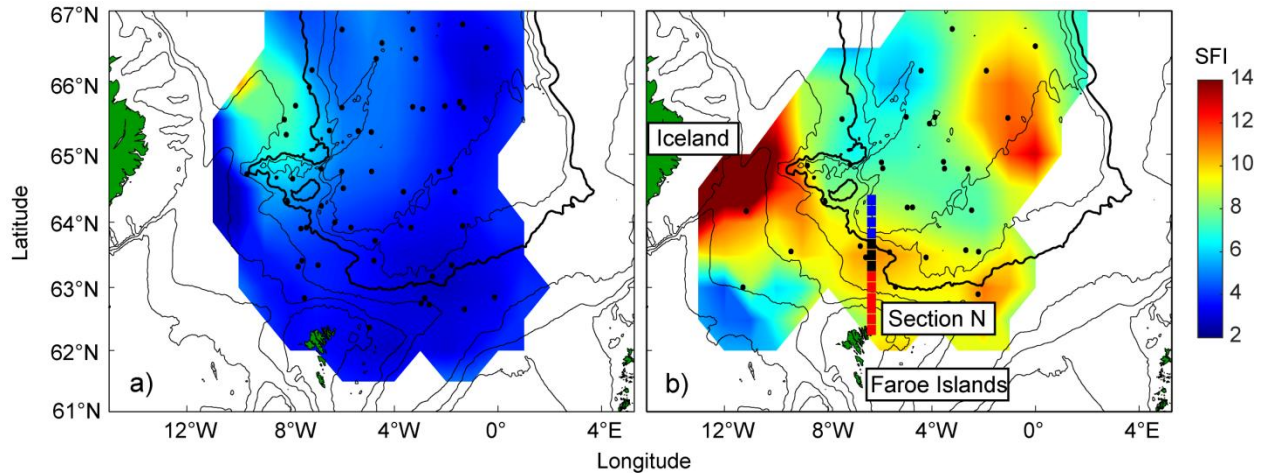


Fig. 18. Mean stomach fullness index (SFI) in (a) 2007-2011 and (b) 2017-2020. The central region along Section N (black) indicates typical frontal stations. Stations within Atlantic water and subarctic water are shown red and blue, respectively. The black dots show the positions where stomach samples were collected.

### 3.5.3 Prey availability in relation of herring distribution

From the mid-1990s, the feeding distribution of the older herring in May can be divided into four periods (ICES, 2020; Eliassen et al., in prep). From 1996-1998, the oldest herring was found in the central and western Norwegian Sea. During the period 1999-2003/2004, the stock abruptly remained northwest of 66°N. In 2003, and more progressively in 2005, the oldest herring has again been aggregation in the southwestern Norwegian Sea to feed. Keeping in mind the variable (i) feeding pattern of herring, (ii) MEIW and (iii) northern *Calanus* spp. abundance (Fig. 12), the prey availability have been averaged into the following four periods, 1996-1998, 1999-2002, 2003-2015 and 2016-2020 (Fig. 19).

In 1996-1998, there was increased prey availability within the EIC and along the JMR (Fig. 19a), but due to the polar conditions in the EIC (~0°C; Malmberg and Valdimarsson, 2003), the herring was only found along the eastern side of the JMF (Holst et al., 2002). The northeastward displacement of the herring distribution (Holst et al., 1999; Eliassen et al., in prep) coincided with an increased flow of EIW/MEIW into the Norwegian Sea (Paper II, ICES, 2020; Skagseth et al., in prep). The sustained high flow of nutrient-rich waters from the west, containing increased zooplankton concentrations, feeds into a positive loop within the Norwegian Sea. The number of overwintering stages increases, and thus the production the following spring, which in turn is continuously supplied with waters from the west. It is likely that this caused the increase in the zooplankton biomass within the Norwegian Sea from 1999-2002 (Fig. 19b), resulting in a shorter route to the new feeding grounds with high prey availability.

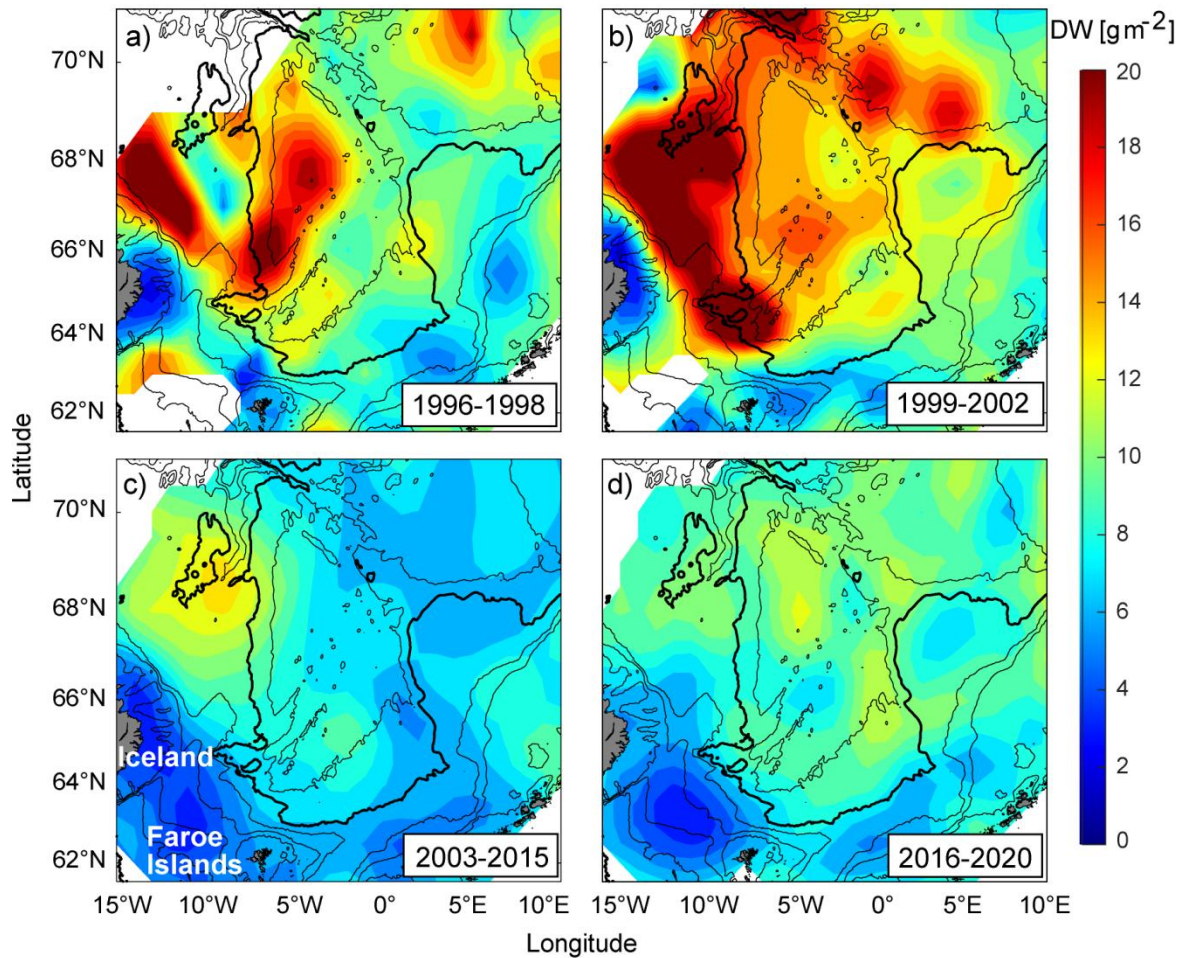


Fig. 19. Mean biomass of zooplankton distribution in May (Dry Weight, grams per square meter), divided into four periods. A) 1996-1998, B) 1999-2002, B) 2003-2015 and D) 2016-2020. The 200, 500, 1000, 2000 (bold) and 3000 m depth contours are shown.

Since ~2003, the herring has continued to migrate to the same location within the southwestern Norwegian Sea, despite the reversal of increased availability of large *Calanus* spp. (Fig. 12), and overall zooplankton biomass, from around 2016 within the wider region (Fig. 19d). During the recent sharp drop in salinity, the temperature has not declined in parallel (Fig. 9; Holliday et al., 2020; ICES, 2020a). Therefore, we suggest that the rather unchanged herring distribution in May since post-2015 is due to continuous favorable temperature within the western region which surpasses a possible effect of increased food concentrations within the Norwegian Sea since 2016.

There are many other aspects of herring behavior to detangle in order to understand their feeding pattern such as inherent learned behaviour between generations, recruitment, stock structure, i.e. age variations and stock size (Fernö et al., 1998). For instance, there is a positive relationship between stock size and distribution area. Therefore, the strong year classes that

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started feeding in the Norwegian Sea in 1999 and 2005 could be important contributors to the changed migration pattern during these periods (Eliassen et al., in prep). Increase in stock size and stock density is also contributing to increased feeding pressure, which warrants further research in relation to the influx of arctic water from the western region and the associated prey.

## 4.0 Summary and Outlook

### 4.1 Summary

The main findings of this study are summarized below.

The *Calanus finmarchicus* individuals along Section N are two separate populations influenced by different current systems. A sudden phenological shift in stage composition, in May, from a decrease of large overwintering and increase of young individuals of *C. finmarchicus* north of the Iceland-Faroe Front occurred in 2003. The shift resulted in an increased numbers of larger individuals during the August/September survey and the release of a production of a second generation.

A sudden reduction in the abundance of *C. hyperboreus*, north of the IFF, in May, co-occurred with the phenological shift of *C. finmarchicus*.

The sudden reduction in *C. hyperboreus* observed north of the IFF in spring is caused by a reduced eastward extension of the East Icelandic Water/Modified East Icelandic Water (EIW/MEIW). The close positive association suggests that *C. hyperboreus* can be used as a biological indicator species of biogeographic shifts caused by shifting water mass boundaries.

Marked anomalous atmospheric changes in 2003 and a decelerated anticlockwise circulation of the Norwegian Sea gyre coincide with reduced volume influx of EIW/MEIW and the sudden shifts in *Calanus* spp. north of the IFF.

During reduced eastward influence the stage composition of *C. finmarchicus* is similar along Section N. The egg production per female was significantly higher north of the IFF and peaked a month earlier than south of the IFF. Larger female sizes and increased lipid content are likely factors contributing to the higher production efficiency.

Since 2015, a shift towards the pre-2003 conditions is observed in the *Calanus* spp., i.e. the abundance of *C. hyperboreus* and large *C. finmarchicus* stages has increased, along with a stronger influence of EIW/MEIW.

The core of the western feeding region for herring in May 2020, i.e. the area with highest zooplankton biomass, was located within the subarctic waters immediately north/west of the junction between the IFF and the Jan Mayen Front. The core area was mainly represented by overwintering stages and the derived adult stages of *C. finmarchicus* and *C. hyperboreus*.

Increased stomach fullness was observed during stronger influx years compared to weaker influx years. This suggests the food availability for herring in May is highly dependent upon the variable eastward intrusion of the arctic waters from the western region.

## 4.2 Outlook

The study has triggered new scientific questions that should be addressed in order to advance our understanding of the *Calanus* spp. variability in the marine climate. These are as follows:

Analyzing female gonad development before and after 2003 would greatly add to our understanding of the phenological shift in stage composition within the subarctic waters, north of the IFF.

The results from the female egg production and the associated variables were challenging to detangle south of the Iceland-Faroe Front. Further seasonal studies could help to clarify if food suppresses the egg production rates or if the decoupling between ascent and initiation of the spring bloom is more important.

A seasonal lipid time-series is unique. Due to high variation in the data presented, more data material would (i) boost the validity of the results and (ii) give clarity to the potential role of wax ester fullness as a trigger for ascent and descent in two contrasting environments.

The variable transport of the Modified East Icelandic Water is known to enter the Faroe Shetland Channel at intermediate depths. It remains to be investigated whether this variability is also observed in the abundance of *Calanus hyperboreus* downstream from the area investigated.

Overflow that enters the Faroe Shetland Channel is either transported via a recently discovered pathway from the Iceland Sea and along the northern boundary of the Iceland-Faroe Ridge (Semper et al., 2020) or from the Norwegian Slope (Chafik et al., 2020). The prevailing pathway is linked to the atmospheric conditions via its regulation of the basin circulation in the Norwegian Sea. As these are the same mechanisms that influence the abundance of *Calanus hyperboreus* within the southwestern Norwegian Sea, it should be further investigated whether *Calanus hyperboreus* could also be used as a biological tracer for the overflow.

Investigating the composition and biomass of the herring diet within the southeastern Iceland Sea would greatly supplement the findings presented in Paper IV as these herring individuals have crossed the Jan Mayen Front immediately upstream from the southwestern Norwegian Sea. Furthermore, comparing the diet from contrasting years would also be new valuable information to aid the understanding of the herring migrations.

Investigation the temperature conditions along the JMF to determine the presence of a heated surface layer since the mid-1990s would aid in detangling the importance of temperature and food availability in relation to herring feeding distribution.

Investigating the carrying capacity of zooplankton biomass for large planktivorous fish stocks would also be a next natural step to investigate.



## References

- Astthorsson, Ó., Hallgrímsson, I., and Jónsson, G. (1983). Variations in zooplankton densities in Icelandic waters in spring during the years 1961-1982. *Rit Fiskid.* 7, 73–113.
- Astthorsson, O. S., and Gislason, A. (1995). Long-term changes in zooplankton biomass in Icelandic waters in spring. *ICES J. Mar. Sci.* 52, 657–668. doi:10.1016/1054-3139(95)80079-4.
- Astthorsson, O. S., and Gislason, A. (2003). Seasonal variations in abundance, development and vertical distribution of *Calanus finmarchicus*, *C. hyperboreus* and *C. glacialis* in the East Icelandic Current. *J. Plankton Res.* 25, 843–854. doi:10.1093/plankt/25.7.843.
- Bagøien, E., Melle, W., and Kaartvedt, S. (2012). Seasonal development of mixed layer depths, nutrients, chlorophyll and *Calanus finmarchicus* in the Norwegian Sea - A basin-scale habitat comparison. *Prog. Oceanogr.* 103, 58–79. doi:10.1016/j.pocean.2012.04.014.
- Blindheim, J., Borovkov, V., Hansen, B., Malmberg, S., and Turrell, W. R. (2000). Upper layer cooling and freshening in the Norwegian Sea in relation to atmospheric forcing. *Deep Sea Res. I* 47, 655–680. doi:10.1016/S0967-0637(99)00070-9.
- Broms, C., and Melle, W. (2007). Seasonal development of *Calanus finmarchicus* in relation to phytoplankton bloom dynamics in the Norwegian Sea. *Deep. Res. Part II* 54, 2760–2775. doi:10.1016/j.dsr2.2007.08.021.
- Broms, C., Melle, W., and Horne, J. K. (2012). Navigation mechanisms of herring during feeding migration: the role of ecological gradients on an oceanic scale. *Mar. Biol. Res.* 8, 461–474. doi:10.1080/17451000.2011.640689.
- Broms, C., Melle, W., and Kaartvedt, S. (2009). Oceanic distribution and life cycle of *Calanus* species in the Norwegian Sea and adjacent waters. *Deep Sea Res. II* 56, 1910–1921. doi:10.1016/j.dsr2.2008.11.005.
- Campbell, R. G., Wagner, M. M., Teegarden, G. J., Boudreau, C. A., and Durbin, E. G. (2001). Growth and development rates of the copepod *Calanus finmarchicus* reared in the laboratory. 221, 161–183.
- Chafik, L., Hátún, H., Kjellsson, J., Larsen, K. M. H., Rossby, T., and Berx, B. (2020). Discovery of an unrecognized pathway carrying overflow waters toward the Faroe Bank Channel. *Nat. Commun.* 11, 1–10. doi:10.1038/s41467-020-17426-8.
- Conover, R. J., and Corner, E. D. S. (1968). Respiration and nitrogen excretion by some marine zooplankton in relation to their life cycles. *J. Mar. Biol. Assoc. United Kingdom* 48, 49–75.
- Dalpadado, P., Ellertsen, B., Melle, W., and Dommasnes, A. (2000). Food and feeding conditions of Norwegian spring-spawning herring (*Clupea harengus*) through its feeding migrations. *ICES J. Mar. Sci.* 57, 843–857. doi:10.1006/jmsc.2000.0573.
- de Jong, M. F., Sjøiland, H., Bower, A. S., and Furey, H. H. (2018). The subsurface circulation of the Iceland Sea observed with RAFOS floats. *Deep. Res. Part I* 141, 1–10. doi:10.1016/j.dsr.2018.07.008.
- Drange, H., Dokken, T., Furevik, T., Gerdes, R., Berger, W., Nesje, A., et al. (2005). “The Nordic Seas: An Overview,” in *The Nordic Seas: An Integrated Perspective*, eds. H. Drange, T. Dokken, T. Furevik, R. Gerdes, and W. Berger (Wash. DC: AGU Geophysical Monograph Series), 1–10.
- Falk-Petersen, S., Mayzaud, P., Kattner, G., and Sargent, J. R. (2009). Lipids and life strategy of Arctic *Calanus*. *Mar. Biol. Res.* 5, 18–39. doi:10.1080/17451000802512267.
- Fernö, A., Pitcher, T. J., Melle, W., Nøttestad, L., Mackinson, S., Hollingworth, C., et al. (1998). The challenge of the herring in the Norwegian Sea: Making optimal collective spatial

- decisions. *Sarsia* 83, 149–167. doi:10.1080/00364827.1998.10413679.
- Gaard, E. (1996). Life cycle, abundance and transport of *Calanus finmarchicus* in Faroese waters. *Ophelia* 44, 59–70. doi:10.1080/00785326.1995.10429839.
- Gaard, E. (2000). Seasonal abundance and development of *Calanus finmarchicus* relation to phytoplankton and hydrography on the Faroe Shelf. *ICES J. Mar. Sci.* 57, 1605–1611. doi:10.1006/jmsc.2000.0963.
- Gislason, A. (2018). Life cycles and seasonal vertical distributions of copepods in the Iceland Sea. *Polar Biol.* doi:10.1007/s00300-018-2392-4.
- Gislason, A., and Astthorsson, O. S. (2002). The food of Norwegian spring-spawning herring in the western Norwegian Sea in relation to the annual cycle of zooplankton. *Sarsia* 87, 236–247. doi:10.1080/00364820260294860.
- Gislason, A., and Silva, T. (2012). Abundance, composition and development of zooplankton in the Subarctic Iceland Sea in 2006, 2007, and 2008. *ICES J. Mar. Sci.* 69, 1263–1276. doi:10.1093/icesjms/fss070.
- Hansen, B., and Østerhus, S. (2000). North Atlantic - Nordic Seas exchanges. *Prog. Oceanogr.* 45, 109–208. doi:10.1016/S0079-6611(99)00052-X.
- Hátún, H., and Chafik, L. (2018). On the Recent Ambiguity of the North Atlantic Subpolar Gyre Index. *J. Geophys. Res.* 123, 1–5. doi:10.1029/2018JC014101.
- Hátún, H., Lohmann, K., Matei, D., Jungclaus, J. H., Pacariz, S., Bersch, M., et al. (2016). An inflated subpolar gyre blows life toward the northeastern Atlantic. *Prog. Oceanogr.* 147, 49–66. doi:10.1016/j.pocean.2016.07.009.
- Hátún, H., and McClimans, T. A. (2003). Monitoring the Faroe Current using altimetry and coastal sea-level data. *Cont. Shelf Res.* 23, 859–868. doi:10.1016/S0278-4343(03)00059-1.
- Hátún, H., Sandø, A. B., Drange, H., Hansen, B., and Valdimarsson, H. (2005). Influence of the Atlantic subpolar gyre on the thermohaline circulation. *Science (80-. )*. 309, 1841–1844. doi:10.1126/science.1114777.
- Head, E. J. H., Harris, L. R., Ringuette, M., and Campbell, R. W. (2013). Characteristics of egg production of the planktonic copepod, *Calanus finmarchicus*, in the Labrador Sea: 1997–2010. *J. Plankton Res.* 35, 281–298. doi:10.1093/plankt/fbs097.
- Heath, M., Boyle, P., Gislason, A., Gurney, W., Hay, S., Head, E., et al. (2004). Comparative ecology of over-wintering *Calanus finmarchicus* in the northern North Atlantic, and implications for life-cycle patterns. *ICES J. Mar. Sci.* 61, 698–708. doi:10.1016/j.icesjms.2004.03.013.
- Heath, M., Fraser, J. G., Gislason, A., Hay, S. J., Jónasdóttir, S. H., and Richardson, K. (2000a). Winter distribution of *Calanus finmarchicus* in the Northeast Atlantic. *ICES J. Mar. Sci.* 57, 1628–1635. doi:10.1006/jmsc.2000.0978.
- Heath, M. R., Astthorsson, O. S., Dunn, J., Ellertsen, B., Gaard, E., Gislason, A., et al. (2000b). Comparative analysis of *Calanus finmarchicus* demography at locations around the Northeast Atlantic. *ICES J. Mar. Sci.* 57, 1562–1580. doi:10.1006/jmsc.2000.0950.
- Heath, M. R., and Jónasdóttir, S. H. (1999). Distribution and abundance of overwintering *Calanus finmarchicus* in the Faroe - Shetland Channel. *Fish. Oceanogr.* 8, 40–60. doi:10.1046/j.1365-2419.1999.00012.x.
- Helland-Hansen, B., and Nansen, F. (1909). The Norwegian Sea - Its physical oceanography based upon the Norwegian researches 1900–1904.
- Hirche, H. J. (1997). Life cycle of the copepod *Calanus hyperboreus* in the Greenland Sea. *Mar. Biol.* 128, 607–618. doi:10.1007/s002270050127.

- Holliday, N. P., Bersch, M., Berx, B., Chafik, L., Cunningham, S., Florindo-López, C., et al. (2020). Ocean circulation causes the largest freshening event for 120 years in eastern subpolar North Atlantic. *Nat. Commun.* 11. doi:10.1038/s41467-020-14474-y.
- Holliday, N. P., Hughes, S. L., Bacon, S., Beszczynska-Möller, A., Hansen, B., Lavín, A., et al. (2008). Reversal of the 1960s to 1990s freshening trend in the northeast North Atlantic and Nordic Seas. *Geophys. Res. Lett.* 35, L03614. doi:10.1029/2007GL032675.
- Holst, J. C., Blindheim, J., Couperus, B., Hammer, C., Jákupsstovu, H., Melle, W., et al. (1999). Report on surveys of the distribution, abundance and migrations of the Norwegian spring-spawning herring, other pelagic fish and the environment of the Norwegian Sea and adjacent waters in late winter, spring and summer of 1999. doi:10.13140/RG.2.2.24583.60323.
- Holst, J. C., Dragesund, O., Hamre, J., Misund, O. A., and Østvedt, O. J. (2002). Fifty years of herring migrations in the Norwegian Sea. *ICES Mar. Sci. Symp.* 215, 352–360.
- Holst, J. C., Røttingen, I., and Melle, W. (2004). “The Herring,” in *The Norwegian Sea Ecosystem*, ed. H. R. Skjoldal (Trondheim: Tapir Academic Press), 203–226.
- Hurrell, J. W. (1995). Decadal Trends in the North Atlantic Oscillation: Regional Temperatures and Precipitation. *Science (80- )*. 269, 676–679. doi:10.1126/science.269.5224.676.
- ICES (2018). Report of the Working Group on International Pelagic Surveys (WGIPS). ICES WGIPS Report 2018 15–19 January 2018. Den Helder, Netherlands. 340pp.
- ICES (2020). Working Group on the Integrated Assessments of the Norwegian Sea (WGINOR; outputs from 2019 meeting). ICES Scientific Reports. 2:29. 46 pp. doi:10.17895/ices.pub.5996.
- Ingvarsdóttir, A., Houlihan, D. F., Heath, M. R., and Hay, S. J. (1999). Seasonal changes in respiration rates of copepodite stage V *Calanus finmarchicus* (Gunnerus). *Fish. Oceanogr.* 8, 73–83. doi:10.1046/j.1365-2419.1999.00002.x.
- Jakobsen, P. K., Ribergaard, M. H., Quadfasel, D., Schmith, T., and Hughes, C. W. (2003). Near-surface circulation in the northern North Atlantic as inferred from Lagrangian drifters: Variability from the mesoscale to interannual. *J. Geophys. Res.* 108, 3251. doi:10.1029/2002JC001554.
- Jakobsson, J., and Østvedt, O. J. (1996). A Preliminary Review of Joint Investigations on the Distribution of Herring in the Norwegian and Iceland Seas 1950-1970.
- Ji, R., Edwards, M., Mackas, D. L., Runge, J. A., and Thomas, A. C. (2010). Marine plankton phenology and life history in a changing climate: current research and future directions. *J. Plankton Res.* 32, 1355–1368. doi:10.1093/plankt/fbq062.
- Jónasdóttir, S. H., Visser, A. W., Richardson, K., and Heath, M. R. (2015). Seasonal copepod lipid pump promotes carbon sequestration in the deep North Atlantic. *Natl. Acad. Sci.* 112, 12122–12126. doi:10.1073/pnas.1512110112.
- Jónasdóttir, S., Richardson, K., Heath, M. R., Ingvarsdóttir, A., and Christoffersen, A. (2008). Spring production of *Calanus finmarchicus* at the Iceland – Scotland Ridge. *Deep. Res. Part I* 55, 471–489. doi:10.1016/j.dsr.2007.12.009.
- Kvamme, C., Nøttestad, L., Fernö, A., and Misund, O. A. (2003). Migration patterns in Norwegian spring-spawning herring: why young fish swim away from the wintering area in late summer. *Mar. Ecol. Prog. Ser.* 247, 197–210. doi:10.3354/meps247197.
- Larsen, K. M. H., Hátun, H., Hansen, B., and Kristiansen, R. (2012). Atlantic water in the Faroe area: sources and variability. *ICES J. Mar. Sci.* 69, 802–808. doi:10.1093/icesjms/fst048.
- Malmberg, S. A. (1969). Hydrographic conditions in the waters between Iceland and Jan Mayen

- in the last decade. *Jokull* 19, 30–43.
- Malmberg, S. A., Thórdardóttir, T., and Vilhjálmsson, H. (1966). Report on the joint survey meeting on the Atlanto-Scandian herring distribution, held at Akureyri, June 12-14, 1966. C.M. 19966/H:18.
- Malmberg, S. A., and Valdimarsson, H. (2003). Hydrographic conditions in Icelandic waters, 1990-1999. *ICES J. Mar. Sci.* 219, 50–60.
- Melle, W., Klevjer, T., Strand, E., Wiebe, P. H., Slotte, A., and Huse, G. (2020). Fine-scale observations of physical and biological environment along a herring feeding migration route. *Deep. Res. Part II* 180. doi:10.1016/j.dsr2.2020.104845.
- Miller, C. B., and Tande, K. S. (1993). Stage duration estimation for *Calanus* populations, a modelling study. *Mar. Ecol. Prog. Ser.* 102, 15–34.
- Misund, O. A., Melle, W., and Fernö, A. (1997). Migration behaviour of norwegian spring spawning herring when entering the cold front in the norwegian sea. *Sarsia* 82, 107–112. doi:10.1080/00364827.1997.10413644.
- Mork, K. A., Skagseth, Ø., Ivshin, V., Ozhigin, V., Hughes, S. L., and Valdimarsson, H. (2014). Advective and atmospheric forced changes in heat and fresh water content in the Norwegian Sea, 1951–2010. *Geophys. Res. Lett.* 41, 6221–6228. doi:10.1002/2014GL061038. Received.
- Niehoff, B., Klenke, U., Hirche, H. J., Irigoien, X., Head, R., and Harris, R. (1999). A high frequency time series at Weathership M, Norwegian Sea, during the 1997 spring bloom: the reproductive biology of *Calanus finmarchicus*. *Mar. Ecol. Prog. Ser.* 176, 81–92. doi:10.3354/meps176081.
- Nielsen, J. E. Ø. (2016). The North Atlantic and Nordic Seas hydrography collection, NERSC Technical Report 372. Nansen Environmental and Remote Sensing Centre, N-5006 Bergen, Norway.
- Nøttestad, L., Misund, O. A., Melle, W., Ulvestad, B. K. H., and Orvik, K. A. (2007). Herring at the Arctic front: influence of temperature and prey on their spatio-temporal distribution and migration. *Mar. Ecol.* 28, 123–133. doi:10.1111/j.1439-0485.2007.00182.x.
- Østvedt, O. J. (1965). The migration of Norwegian herring to Icelandic waters and the environmental conditions in May-June 1961-1964. *Fisk. Skr. Ser. Havundersøkelser* 13, 29–47.
- Pavshitsk, E. A. (1956). Seasonal changes in plankton and feeding migrations of herring. Trudy PINRO. 99, 104-140 (in Russian).
- Poulain, P., and Warn-Varnas, A. (1996). Near-surface circulation of the Nordic seas as measured by Lagrangian drifters. *J. Geophys. Res.* 101, 18,237-18,258. doi:10.1029/96JC00506.
- Read, J. F., and Pollard, R. T. (1992). Water masses in the region of the Iceland–Færoes Front. *J. Phys. Oceanogr.* 22, 1365–1378. doi:10.1175/1520-0485(1992)022<1365:WMITRO>2.0.CO;2.
- Richter, K., and Maus, S. (2011). Interannual variability in the hydrography of the Norwegian Atlantic Current: Frontal versus advective response to atmospheric forcing. *J. Geophys. Res. Ocean.* 116, 1–13. doi:10.1029/2011JC007311.
- Richter, K., Segtnan, O. H., and Furevik, T. (2012). Variability of the Atlantic inflow to the Nordic Seas and its causes inferred from observations of sea surface height. *J. Geophys. Res.* 117, C04004. doi:10.1029/2011JC007719.
- Semper, S., Pickart, R. S., Våge, K., Larsen, K. M. H., Hátún, H., and Hansen, B. (2020). The

- Iceland-Faroe Slope Jet: a conduit for dense water toward the Faroe Bank Channel overflow. *Nat. Commun.* 11, 1–10. doi:10.1038/s41467-020-19049-5.
- Serra, N., Käse, R. H., Köhl, A., Stammer, D., and Quadfasel, D. (2010). On the low-frequency phase relation between the Denmark Strait and the Faroe-Bank Channel overflows. *Tellus A* 62, 530–550. doi:10.1111/j.1600-0870.2010.00445.x.
- Skagseth, Ø., and Mork, K. A. (2012). Heat content in the Norwegian Sea, 1995-2010. *ICES J. Mar. Sci.* 69, 826–832. doi:10.1093/icesjms/fss026.
- Skjoldal, H. R., Sætre, R., Færnø, A., Misund, O. A., and Røttingen, I. eds. (2004). *The Norwegian Sea Ecosystem*. Trondheim: Tapir Academic Press.
- Søiland, H., and Huse, G. (2012). Using RAFOS floats to simulate overwinter transport of *Calanus finmarchicus* in the Norwegian Sea. *Mar. Biol. Res.* 8, 502–507. doi:10.1080/17451000.2011.639780.
- Stenevik, E., Melle, W., Gaard, E., Gislason, A., Broms, C. T. Å., Prokopchuk, I., et al. (2007). Egg production of *Calanus finmarchicus* - A basin-scale study. *Deep Sea Res. Part II* 54, 2672–2685. doi:10.1016/j.dsr2.2007.08.027.
- Strand, E., Bagøien, E., Edwards, M., Broms, C., and Klevjer, T. (2020). Spatial distributions and seasonality of four *Calanus* species in the Northeast Atlantic. *Prog. Oceanogr.* 185. doi:10.1016/j.pocean.2020.102344.
- Thórdardóttir, T. (1977). Primary production in north Icelandic waters in relations to recent climatic changes. in *Polar Oceans*, ed. M. J. Dunbar (Canada: Proceedings Ocean Congress Montreal 1974), 655–665.
- WGINOR (2018). ICES WGINOR REPORT 2018 Report of the Working Group on Integrated Ecosystem Assessments for the Norwegian Sea (WGINOR).
- Wiborg, K. F. (1955). Zooplankton in relation to hydrography in the Norwegian Sea. *Fisk. Skr. Ser. Havundersøkelser.* 11, 1–66. doi:hdl.handle.net/11250/114534.
- Zhai, L., Gudmundsson, K., Miller, P., Peng, W., Guðfinnsson, H., Debes, H., et al. (2012). Phytoplankton phenology and production around Iceland and Faroes. *Cont. Shelf Res.* 37, 15–25. doi:10.1016/j.csr.2012.01.013.