PhD in Aquatic Biosciences // No. 21 - 2017

Interannual variability in key zooplankton species in the North-East Atlantic: an analysis based on abundance and phenology

Marina Espinasse

FACULTY OF BIOSCIENCES AND AQUACULTURE

NORD University

www.nord.no

Interannual variability in key zooplankton species in the North-East Atlantic: an analysis based on abundance and phenology

Marina Espinasse

A thesis for the degree of
Philosophiae Doctor (PhD)

PhD in Aquatic Biosciences no. 21 (2017)
Faculty of Biosciences and Aquaculture

PhD in Aquatic Biosciences no. 21 (2017)

Marina Espinasse
Interannual variability in key zooplankton species in the North-East
Atlantic: an analysis based on abundance and phenology

ISBN: 978-82-93165-20-0

Print: Trykkeriet NORD

Nord University
N-8049 Bodø
Tel: +47 75 51 72 00
www.nord.no

Preface

This dissertation has been submitted in fulfilment of the requirements for the degree of Philosophiae Doctor (PhD) at the faculty of Biosciences and Aquaculture (FBA), Nord University. The original research presented in the dissertation was carried out from 15.04.2013 through 01.09.2017 as a part of the Northern Area program funded by Lundin Norway (grant number C000353), Conoco Philips (grant number NSBU-107021), and Nord University. This project was also supported by the ARCTOS research network.

The project team included the following members:

Marina Espinasse, MSc, FBA, Nord University: PhD candidate

Ketil Eiane, Professor, FBA, Nord University: primary supervisor

Claudia Halsband, Senior Researcher, Akvaplan-niva: project leader and co-supervisor

Øystein Varpe, Professor, The University Centre in Svalbard/Akvaplan-niva: co-supervisor

Marina Espinasse
Bodø, 26th of October 2017

Acknowledgements

Reaching the defence of the PhD thesis was a long and difficult journey. I believe that successful finale of this journey would not have been possible without some, very special people around me. I would like to express my deepest thanks to all of them here.

First, I wish to greatly thank all my supervisors, Claudia Halsband, Ketil Eiane, Øystein Varpe, Astthor Gislason, Kristinn Gudmundsson, and Stig Falk-Petersen. I wish to thank them all for giving me an opportunity to work on this project, for their guidance, patience and expertise. I would like to especially thank Ketil Eiane for his outstanding optimism and his big heart. He always managed to make me believe in success, when my confidence dropped to zero. I am also very thankful to zooplankton team of the Marine and Freshwater Institute in Iceland - Solrunn, Hildur, and Teresa, for that they made my three months in Reykjavik unforgettably good yet efficient. I am thankful to Malin Daase, who, being a very busy scientist, always found time to answer my questions and help me with data analysis. I appreciate the help of Daria Martynova and Nikolay Usov, my Russian colleagues, for sharing the data and giving valuable advices for the parts of the PhD project.

I highly appreciate the very friendly environment at Nord University that was created and maintained by the nicest people in the Northern Hemisphere: Kanchana, Prabhu, Marc, Sunnje, Andrea, Cecilia, Anusha, Cindy, Shruti, Deepti, Helene, Michael, Amalia and many others who I shared the PhD corridors and kitchens with! I want to give special thanks to Marvin, Irina and Alex, who were not just friends and not just colleagues. They are people that I deeply respect and enjoy being close to.

I will not forget the welcoming team of the Faculty for Biosciences and Aquaculture. I want to express my gratitude to Nina, Reid, Jenanett, Irene, Randi and all the administration staff of the faculty who guaranteed my comfort at the university and helped me to practice Norwegian.

I want to greet my Russian friends in Bodø, Tromsø, and Oslo - Lesja, Maria R., Alisa, Irina, Katja, Maria K., for our interesting discussions, litres of Russian tea and numerous

sweets that we had together. You all made my life in Norway “nearly Russian” and you made me feel happy and relaxed in this country.

Lastly, I want to give warm thanks to my family and friends in Russia, which have supported me all the way towards the PhD defence. My final and very special thanks go to Boris, my closest person, who encouraged me to continue the PhD work and who brought me to the highest tops I have ever been – in literal and figurative meaning.

The Open University, UK

Table of contents

List of figures

List of papers

Paper I	Skreslet S, Olsen K, **Chelak M**, Eiane K. (2015) NE Atlantic zooplankton wintering in fjord habitats responds to hemispheric climate J Plankton Res 37:773-789
Paper II	**Espinasse M**, Halsband C, Varpe Ø, Gislason A, Gudmundsson K, Falk-Petersen S, Eiane K. (2017) The role of local and regional environmental factors for *Calanus finmarchicus* and *C. hyperboreus* abundances in the Nordic Seas Polar Biol. (Accepted on June 19th, 2017).
Paper III	**Espinasse M**, Halsband C, Varpe Ø, Gislason A, Gudmundsson K, Falk-Petersen S, Eiane K. A comparison of interannual variations in phenology in two North-East Atlantic populations of *Calanus finmarchicus* using vertical life table approach. Manuscript
Paper IV	**Espinasse M**, Halsband C, Varpe Ø, Martynova D, Usov N, Eiane K. A vertical life table approach to copepod phenology: a comparison with horizontal approaches based on *Calanus glacialis* abundance time series in the White Sea, Russia. Manuscript (Short communication).

Abstract

The objective of this Thesis was to enhance the understanding of what drives the variability in zooplankton populations in the North-East Atlantic. I approached this objective by studying the dynamics of key zooplankton species in several locations of the North-East Atlantic. For two locations in northern Norway, I addressed the teleconnections between zooplankton and hemispheric climate variability. I compared variability in zooplankton abundance and phenology between locations and identified relationships between environmental factors and zooplankton population dynamics on both local and large scale. Finally, I evaluated different metrics for quantifying the phenological variability in populations of *Calanus*, and applied them for studying relationships between environmental variability and *Calanus* phenology in the North-East Atlantic.

The Thesis is built on four papers. The focus and the main results of each paper are as follows:

Paper I related abundances of four zooplankton species (*Calanus finmarchicus*, *Calanus hyperboreus*, *Themisto abyssorum*, and *Pareuchaeta norvegica*) in two fjords in northern Norway to regional climatic oscillation in the North Atlantic. Results showed that hemispheric climate regulated overwintering zooplankton populations in the study locations through the effects on local environment in the fjords. Climate effects on zooplankton populations varied between the fjords and reflected the differences in topography of the fjords.

Paper II focused on the interannual abundance variability of *C. finmarchicus* and *C. hyperboreus* in three locations in the North-East Atlantic (a northern Norwegian fjord, the west coast of Svalbard, and northern Icelandic waters). Results indicated that *Calanus'* responses to environmental variability were species- and location-specific, and that climate effects, mediated through water mass advection and bottom-up regulation, were likely important for generating variability in *Calanus* abundances.

Paper III studied the variability in phenology of two *C. finmarchicus* populations – from the western Svalbard shelf and northern Icelandic waters. The phenology of both populations correlated with water temperature, while the phenology of *C. finmarchicus* in Svalbard was also related to large-scale climate variability.

Paper IV applied two types of phenological indices on *C. glacialis* abundance data in the White Sea. Phenological indices based on a vertical life table approach were compared with more commonly used indices based on a horizontal life table approach. The results indicated that vertical phenological indices are at least as sensitive to environmental variability as horizontal indices, and that applicability of different vertical indices depends on the sampling season and the life cycle of the species of interest.

1. Introduction

1.1. The variability of marine zooplankton

In the pelagic marine realm, zooplankton is a numerous and dynamic group of organisms (Bogorov, 1974). Unlike the nekton (swimmers such as fish), the distribution of zooplankton is mainly reflecting transport by ocean currents (Hensen, 1884). This passive dispersion mode renders the distribution of zooplankton sensitive to variability in ocean currents and thus, populations often vary more in abundance and distribution than many other groups of marine metazoans (Miller and Wheeler, 2012).

Many zooplankton species have a life cycle of one to several years, and this comparatively short generation time enables them to respond numerically to environmental changes faster than many other, more long-lived organisms (Hays et al., 2005). Thus, changes in the abundance and distribution of zooplankton may be used as a diagnostic tool in the studies of environmental effects on marine ecosystems (Keister et al., 2012, Mackas et al., 2012, Edwards, 2009).

Indeed, many marine zooplankton species are susceptible to climate variability (Beaugrand, 2005, Hays et al., 2005) and especially, to changes in ambient temperature, as temperature directly affects their physiology (Edwards and Richardson, 2004). This sensitivity to temperature underlies an apparent separation of zooplankton species based on their main distribution pattern, into Boreal and Arctic groups in the North Atlantic (Bogorov, 1974). The implication of this is that in the Arctic regions, the presence of Boreal fauna tends to be limited or represented by expatriated individuals, and *vice versa* (Jaschnov, 1970). Accordingly, some zooplankton species of Arctic or Boreal origin are associated with, and used as an indicator of, distinct water masses of Arctic or Atlantic origin, respectively (Astthorsson et al., 1983, Daase and Eiane, 2007).

To build knowledge of the mechanisms that relate environmental variability to zooplankton distribution the ocean, long-term abundance data-series are highly useful (Richardson, 2008). In the Northern Hemisphere, examples of such data-series include the Continuous Plankton Recorder survey (CPR) in the North Atlantic (e.g., Beare et al., 2003), the California Cooperative Oceanic Fisheries Investigation (e.g., Ohman and Smith, 1995), and the Odate collection in the Pacific Ocean (e.g., Chiba, 2005).

Such data-series contain information on several zooplankton species. Most studies, however, focus on calanoid copepods, and in particular, on the genus *Calanus*, due to the wide distribution and high abundance of this taxon throughout the North Atlantic and North Pacific (Brodsky et al., 1983) and its prominent role in the energy flow of high latitude pelagic ecosystems (Melle et al., 2004). *Calanus* is used as a model organism in studies of environmental effects on zooplankton populations (Fromentin and Planque, 1996, Greene and Pershing, 2007, Kvile et al., 2014) and in the studies of long-term variability in zooplankton abundance (Villarino et al., 2015, Wilson et al., 2016). Following this tradition, this Thesis is based largely on the analysis of *Calanus* spp. abundance data series.

1.2. Analysis of zooplankton data series

A relatively recent direction in the study of zooplankton populations is the use of several decades-long data series and the comparison of multiple data sets in one study (Melle et al., 2014, Head et al., 2013, Gislason et al., 2014, Pepin et al., 2015). The advantage of comparing zooplankton data-series from different locations is that it allows for improved understanding of zooplankton variability over large geographical scales (Perry et al., 2004, Richardson and Schoeman, 2004). Such studies may help to disentangle the roles of environmental variables for zooplankton variability and to identify common drivers of such variability (Mackas et al., 2012). Large-scale comparisons of long-term data series also allow for determination of spatial and temporal scales within which similar patterns of zooplankton population dynamics are observable (Batchelder et al., 2012).

However, large-scale comparisons of zooplankton variability are often complicated by limited data availability, especially in the high latitude regions, where many zooplankton species tend to be particularly sensitive to environmental factors (Weydmann et al., 2013, Søreide et al., 2010, Daase et al., 2013). When seasonal development of zooplankton is of interest, there is often a requirement for temporally well-resolved data, ideally covering the full development of an organism. In addition, information on environmental variability that may bias interpretation, such as advection of water masses, temperature and predation (Gentleman et al., 2012, Gentleman et al., 2008) should ideally accompany abundance data.

Such data, unfortunately, are rare, but several approaches to overcome poor data quality are available. Examples include Generalized Modelling techniques (Wood, 2006), that allow for accounting for spatial and temporal variability in the data and other random effects that are usually inherent in the long-term data series. Such statistical models were successfully employed for predicting distribution changes and abundance variability of zooplankton in the North Atlantic (Villarino et al., 2015, Chust et al., 2013, Carstensen et al., 2012, Dupont et al., 2017). Other approaches are numerical simulation models designed to emulate e.g. seasonal processes in zooplankton such as dormancy (Wilson et al., 2016, Maps et al., 2012, Pierson et al., 2013), vertical distribution (Bandara et al., 2016), advection (Kvile et al., 2016, Espinasse et al., 2016, Eisenhauer, 2016) or the whole life history (Varpe et al., 2007, Varpe et al., 2009).

Despite the increasing number of studies and a variety of analytical approaches, the mechanisms connecting zooplankton variability to environmental changes is still an area with many unanswered questions and, therefore, further investigations are needed (Parent et al., 2015, Runge et al., 2015, Maps et al., 2016). Especially, more knowledge is needed about zooplankton populations from high latitudes where large-scale environmental changes such as climate change may be most severe (Wassmann et al., 2011) while, unfortunately, high-quality data sets are little available.

1.3. *Calanus* – a key zooplankton genus in North Atlantic pelagic ecosystems

Copepods of the genus *Calanus* constitute one of the most numerous zooplankton taxa in the North Atlantic Ocean (Brodsky et al., 1983). *Calanus* spp. are a major link between primary production and higher trophic level organisms (Mauchline, 1998) and are a preferred food source for many economically important fish species such as young stages of cod, capelin, herring and mackerel (Last, 1989, Huse and Toresen, 1996, Dalpadado et al., 2000, Darbyson et al., 2003). They also contribute to the biological carbon pump in the ocean, because they largely consume phytoplankton carbon, which is eventually deposited on the seabed as their faecal pellets (Wassmann et al., 2006, Wassmann, 1997).

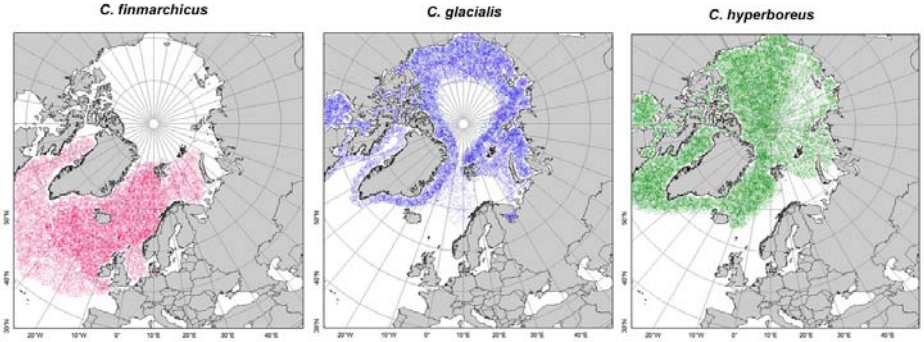


Figure 1. The main distribution areas of *Calanus finmarchicus*, *C. glacialis*, and *C. hyperboreus* (based on Conover (1988) and Jaschnov (1970))

In the northern North Atlantic, the genus *Calanus* is mainly represented by three species*: C. finmarchicus* (Gunnerus 1770), *C. glacialis* Jashnov 1955, and *C. hyperboreus* Krøyer 1838. *C. finmarchicus* has the southern-most distribution in the North Atlantic (Fig. 1), and is considered as an indicator species of Atlantic water masses (Smith et al., 1985, Tande, 1991, Østvedt, 1955, Brodsky et al., 1983). *C. hyperboreus* and *C. glacialis* are mainly Arctic species, with *C. glacialis* occupying mostly shelf areas of the Arctic Ocean and surrounding seas, and *C. hyperboreus* mainly inhabiting oceanic basins in the Arctic (Conover, 1988, Hirche and Kwasniewski, 1997, Richter, 1994) (Fig. 1). All three congeners have a similar life cycle development that includes freely spawned eggs, six naupliar stages (NI –NVI), and five copepodite stages (CI – CV) before the final molt into sexually mature adults (CVI; Fig. 2). However, size, generation time, and reproduction strategies vary between the species (Conover 1988). *C. finmarchicus* typically spawns in spring and has a one-year life cycle, but in the southern Norwegian Sea, subsidiary spawning may occur in late summer (Tande et al., 1985, Wiborg, 1954, Østvedt, 1955). The life cycle of *C. glacialis* may last from one to three years (Tande et al., 1985, Kosobokova, 1999, Niehoff et al., 2002), and reproduction usually occurs prior to, or shortly after the spring phytoplankton bloom (Daase et al., 2013). The *C. hyperboreus* life cycle may take 2 to 5 years to complete, and unlike for the other two congeners, reproduction starts in winter, up to several months before the spring bloom (Hirche and Niehoff, 1996, Plourde et al., 2003).

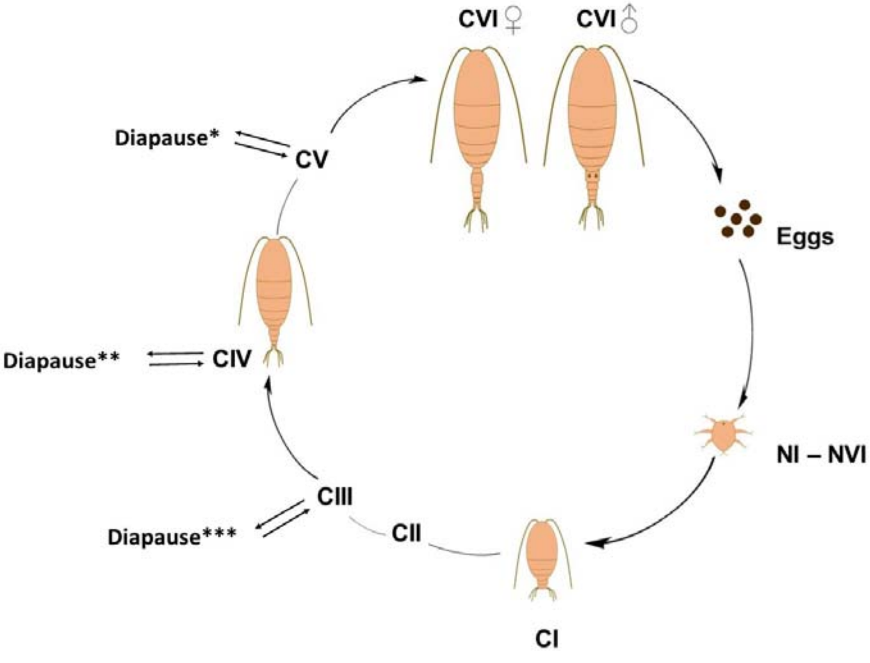


Figure 2. Generalized life cycle of *Calanus* spp. Developmental stages are denoted as NI-NVI, - nauplii stages one through six; CI-CV – copepodite stages one though five, CVI – adults (male and female). * denotes the most common timing of the winter diapause for a one year life cycle (*C. finmarchicus* and sometimes *C. glacialis*); ** indicates timing of the first diapause for a two-year life cycle (*C. glacialis* and *C. hyperboreus*); *** indicates timing of the first diapause for a three-year life cycle (*C. hyperboreus*). Based on Conover (1988).

1.4. Effects of climate variability on the distribution and abundance of *Calanus* in the North Atlantic

Over the last decades, effects of climate variability have been detected in marine ecosystems (Hays et al., 2005, Greene and Pershing, 2007, Barnett et al., 2001, Levitus et al., 2000). Climate variability may cause regime shifts in marine ecosystems characterised by alteration of the oceanic circulation and changes in species abundances and distribution (Greene and Pershing, 2007). Such shifts in marine ecosystems have occurred, for example, in the North Sea (Beaugrand, 2004), in the Norwegian and the Barents Seas (Loeng and Drinkwater, 2007, Matishov et al., 2012), and in the Arctic Ocean (Steele et al., 2008).

Under climate change, the distribution of *C. finmarchicus* is predicted to shift poleward in the North Atlantic (Chust et al., 2013), while C. *hyperboreus* and *C. glacialis* are predicted to decrease in abundance if temperature in the Arctic continues to rise (Carstensen et al., 2012, Henriksen et al., 2012). This is probably due to weak tolerance of *C. glacialis* to thermal stress (Smolina et al., 2015), and increased metabolic rates at elevated temperatures (Grote et al., 2015; Coyle and Gibson 2017). Similarly, for *C. hyperboreus*, elevated sea temperatures and the associated increased metabolic demand can decrease size at maturity and thus, reduce the fecundity (Henriksen et al., 2012, Halvorsen, 2015).

Ecological implication of these changes in *Calanus* distribution and abundance may replace *C. glacialis* and *C. hyperboreus*-mediated food webs with *C. finmarchicus*-based food web in the Arctic (Falk-Petersen et al., 2007). This will likely reduce energetic content of the food for the Arctic marine planktivores such as e.g. the little auk (*Alle alle*) for which *C. hyperboreus* and *C. glacialis* are essential food sources (Karnovsky et al., 2010, Karnovsky et al., 2003), thus decreasing survival or reproduction in this bird populations. Lastly, pelagic ecosystem dominated by smaller sized copepods would be characterized by a faster recycling and a reduced transport of the organic carbon to the deep ocean with yet unknown consequences for marine ecosystems (Beaugrand, 2009).

1.5. Environmental variability and *Calanus* phenology in the North Atlantic

Phenology is the study of the timing of the seasonal development of organisms. Changes in phenology can provide a useful indicator of the species responses to climatic variability (Edwards et al. 2004).

The phenology of *Calanus* may vary with changes in the environment (Mackas et al., 2012). Under warmer climate in the North Atlantic, *C. finmarchicus* is expected to reproduce earlier as well as to have a higher number of generations per year (Head et al., 2013). Variations in water temperature can also affect developmental rates of zooplankton (Ellertsen et al., 1987), and the timing and duration of diapause (Head et al., 2013; Wilson et al., 2016).

Shifting seasonality in *Calanus* may affect recruitment of planktivorous fishes. For example, when the timing of maximum *Calanus* abundance does not coincide with the highest food requirement for fish juveniles, recruitment of the fish stocks decreases (Cushing, 1990). Similarly, the match in the timing of the peak abundance of *C. finmarchicus* and cod juveniles in the North and in the Barents Seas significantly increases the survival of the new generation of cod (Beaugrand et al., 2003, Sundby, 2000). The other consequences of phenological shifts in *Calanus* for pelagic ecosystems are not yet fully understood, and further studies on field data and improved techniques to identify phenological shifts are required (Ji et al., 2010b).

Understanding *Calanus* phenology can be a complicated objective, because phenological responses seem to be non-uniform on larger spatial scales (Poloczanska et al. 2013). For instance, populations in areas characterised by different oceanographic regimes may differ in their phenology, and may have distinct phenological responses to environmental variability (Gislason, 2005, Kvile et al., 2014, Planque et al., 1997). Also, there are indications that populations from core distribution areas may respond differently to changes in the environment than fringe populations (Beaugrand et al., 2014).

In addition, local changes in hydrography, such as variability in the inflow of Atlantic waters, can significantly impact on *Calanus* phenology (Kristiansen et al., 2015), resulting in phenological differences between populations within oceanographic regions.

Overall, this suggests that predictions of phenological changes in *Calanus* should consider both variability in local conditions and regional environmental factors.

1.6. The study areas

The main study areas of this Thesis include data-series obtained from the northern Icelandic shelf, the Norwegian Sea, the Barents Sea, and from the White Sea.

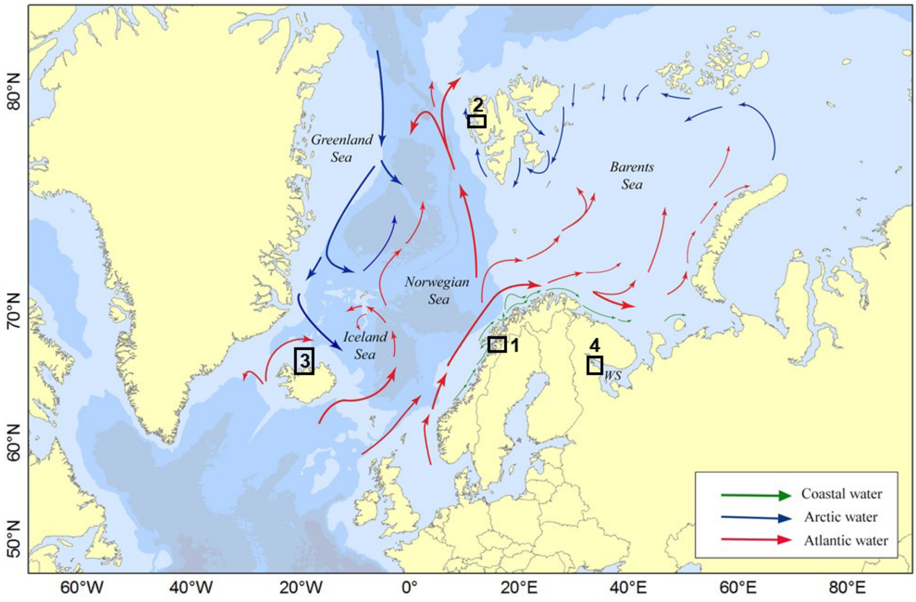


Figure 3. The map of the oceanic circulation in the North-East Atlantic.Green, blue, and red arrows denote respectively, coastal, Arctic and Atlantic water masses. WS stands for the White Sea. The map has been modified after Blindheim et al. (2005) and Loeng and Drinkwater (2007). The rectangles and numbers indicate the sampling locations as follows: 1 – Northern Norway (**Paper I**, **Paper II**); 2 – Western Svalbard shelf (**Paper II**, **Paper III**); 3 – northern Icelandic shelf (**Paper II**, **Paper III**); 4 – the White Sea (**Paper IV**).

The North-East Atlantic is characterized by the influence of Atlantic water masses originating from the Sub-Tropical gyre (Fig. 4). Atlantic waters enter the North-East Atlantic primarily through the Denmark Straight (between Iceland and Greenland), over the Iceland-Faroe Ridge (between Iceland and Faroe Islands), and through the Faroe-Shetland Channel (between the Faroes and the Norwegian Coast) (Aksnes and Blindheim, 1996). The inflow of Atlantic water which continues along the Norwegian coast is the main driver of the thermohaline circulation in the North-East Atlantic (Blindheim et al., 2000), and thus, has a great impact on the marine ecosystems of this area. The main source of Arctic water masses to the North-East Atlantic are the East Greenland current, flowing southwards along the continental slope of Greenland (Blindheim et al., 2005) and, to a lesser extent, the South Cape current flowing along the Svalbard archipelago (Swerpel, 1985).

The Iceland Sea and northern Icelandic waters

The Iceland Sea and northern Icelandic waters are located in the interaction zone between Atlantic and Arctic water masses. Atlantic water masses enter the Iceland Sea and northern Iceland shelf from the south-west of Iceland as the North Icelandic Irminger Current (Valdimarsson and Malmberg, 1999). One branch of this current flows eastwards along northern Iceland shelf, while another branch turns westwards towards the east coast of Greenland. The East Greenland current flows along the west coast of Greenland and while entering the Iceland Sea, it partly mixes with the Atlantic waters of the Northern Icelandic Irminger Current and Atlantic water masses coming from Jan-Mayen area. These modified Arctic waters continue south-westwards along the northern Icelandic continental slope as the East Icelandic Current (Valdimarsson and Malmberg, 1999, Swift and Aagaard, 1981).

The interaction between Atlantic and Polar water masses in northern Icelandic waters and the Iceland Sea forms the Polar Front, but the relative amounts of warm and cold water masses in the front area may vary seasonally and interannually. This variability affects hydrographical and local climatic conditions in northern Iceland (Malmberg and Valdimarsson, 2003, Stefánsson and Gudmundsson, 1969). An intensified inflow of warmer Atlantic waters is associated with increased primary productivity and higher abundances of *C. finmarchicus* (Thórdardóttir, 1984, Astthorsson et al., 1983), while the dominance of Arctic waters in the area is reflected in reduced productivity and higher abundances of Arctic-associated zooplankton such as *C. hyperboreus* and *M. longa* (Astthorsson and Gislason, 1995).

Thus, in the Iceland Sea, oceanographic changes are being relatively quickly reflected in zooplankton variability. This ecosystem, therefore, is a suitable location for studying interannual dynamics in zooplankton species in relation to environmental variability.

The Norwegian Sea

Similar to the northern Icelandic shelf, the ecosystem of the Norwegian Sea is largely affected by Atlantic waters inflow. The main branch of Atlantic water inflow to the Norwegian Sea ecosystem is the Norwegian Atlantic current (NAC), flowing along the coast of Norway and into the Barents Sea. NAC transports boreal zooplankton species such as *C. finmarchicus* into the Norwegian Sea and supports higher primary production than in the areas less affected by Atlantic waters (Aksnes and Blindheim, 1996, Loeng and Drinkwater, 2007).

Interannuall variations in the amount of Atlantic inflow through the NAC tend to reflect large-scale climate fluctuations such as the North Atlantic Oscillation (NAO) (Orvik et al., 2001). During high NAO periods, the volume of the Atlantic water inflow to the Norwegian Sea is larger (Mork and Blindheim, 2000), which increases heat transport and advection of zooplankton to the Norwegian Sea. In addition, cross-sectional area of the outer branch of the NAC is shallower, resulting in a reduced mixed layer depth, which in turn induces an earlier onset of the spring bloom in such years (Blindheim et al., 2000). In years with low NAO, the opposite situation occurs. This variability in the timing of primary production in the Norwegian Sea, is then translated into the variability of zooplankton abundances (Drinkwater et al., 2003).

The Norwegian Sea covers the main distribution area of *C. finmarchcius* in the northern North Atlantic. The Norwegian and the Lofoten Basins of the Norwegian Sea host major overwintering populations of *C. finmarchicus*, from where *C. finmarchicus* is advected by oceanic currents over the Norwegian Sea (Broms et al., 2009, Halvorsen et al., 2003). In addition, Arctic congeners *C. hyperboreus* and *C. glacialis* are also found in the Norwegian Sea, but usually in a lower and less stable abundances (Melle and Skjoldal, 1998).

These characteristics make the Norwegian Sea a particular location to study interannual variability in *Calanus* spp. in relation to both local environment, such as advection, and large-scale climate effects. This is reflected in a large number of fundamental zooplankton studies that include data from the Norwegian Sea (e.g., Melle et al., 2014, Dupont et al., 2017, Melle et al., 2015).

The western Svalbard shelf (Barents Sea)

The western Svalbard shelf is located in the north-western part of the Barents Sea. One of the branches of the Atlantic water inflow from the Norwegian Sea to the Barents Sea from the West Spitsbergen Current or WSC, which flows north-eastwards along the shelf break of the Barents Sea (Loeng, 1991). On the west coast of Svalbard, the inflow of Atlantic water through the WSC plays an important role for the ecosystems of the Western Svalbard shelf. Due to this inflow, the productivity of the area is comparatively high. In addition, WSC transport boreal zooplankton, such as *C. finmarchicus*, to the western Svalbard shelf (Hop et al., 2006, Hop et al., 2002). Accordingly, *C. finmarchicus* is one the most abundant copepods on the western Svalbard shelf, while Arctic copepods, such as *C. glacialis* and *C. hyperboreus*, are found in much lower abundances (Kwasniewski et al., 2003, Hop et al., 2002).

Like in the Norwegian Sea, the inflow of Atlantic waters to the Barents Sea and the western Svalbard shelf responds to NAO variability. Positive NAO anomalies are usually associated with higher water temperature and increased planktonic productivity in the Barents Sea (Ottersen and Stenseth, 2001, Sandø et al., 2010). However, in the Barents Sea and western Svalbard shelf, the responses of marine ecosystems to NAO variability tend to appear after a time-lag of several years (Visbeck et al., 2013, Kwasniewski et al., 2012).

The western Svalbard shelf, therefore, is suitable for studies of effects of both advection and climate on zooplankton populations.

The White Sea

The White Sea is a shelf sea located to the south-west from the Barents Sea. The northern boundary of the White Sea is designated by the line connecting Svyatoy Nos peninsula and Kanin peninsula (Fig. 5). The White Sea is characterised by high freshwater run-off from the rivers and limited water exchange with the Barents Sea, which results in low salinities in the White Sea throughout a year (13 psu to 32 psu) (Babkov and Lukanin, 1985).

Among *Calanus* spp., only an Arctic *C. glacialis* occurs in the White Sea in stably high numbers, with only occasional observations of *C. finmarchicus* (Berger, 2001). This *C. glacialis* population is believed to be a relict population, isolated from the rest of the distributional area of the species since last interglacial period, when North Atlantic waters entered the Barents Sea (Jaschnov, 1970). This makes the White Sea *C. glacialis* a unique population, which ecological adaptation and responses to environmental forcing may differ from the populations in the main distributional area of the species (Beaugrand et al., 2013).

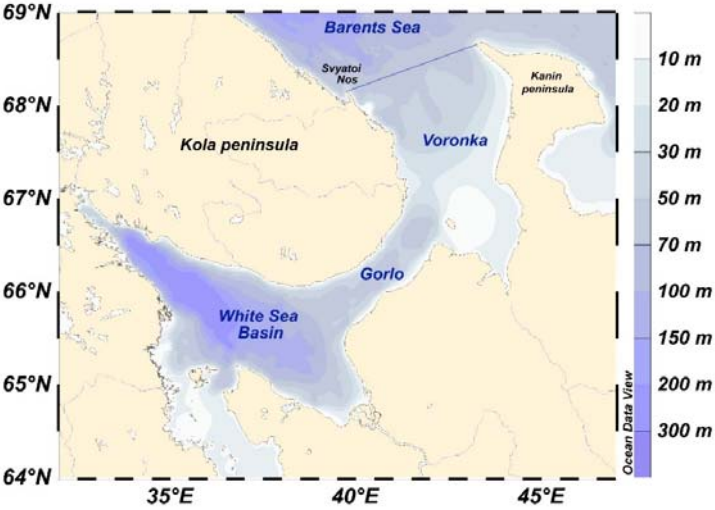


Figure 4. The bathymetry of the White Sea. The borders of the sea and the locations of Voronka, Gorlo and the Basin of the White Sea are indicated.

2. Objectives

The main objective of this Thesis was to study interannual variability in *Calanus* spp. populations and to shed new light on the relationship between environmental variability and zooplankton populations in the North-East Atlantic. Specifically, the Thesis addressed three sub-objectives (Fig. 3):

1) To study how climate variability is related to abundances of overwintering stocks of key zooplankton species in northern Norwegian fjords (**Paper I**).

2) To identify local and large scale environmental factors that drive *Calanus* spp. variability in the North-East Atlantic as well as to identify species- and location-specific responses to environmental variability (**Paper II, Paper III**).

3) To compare different methods to study *Calanus* spp. phenology (**Paper IV**).

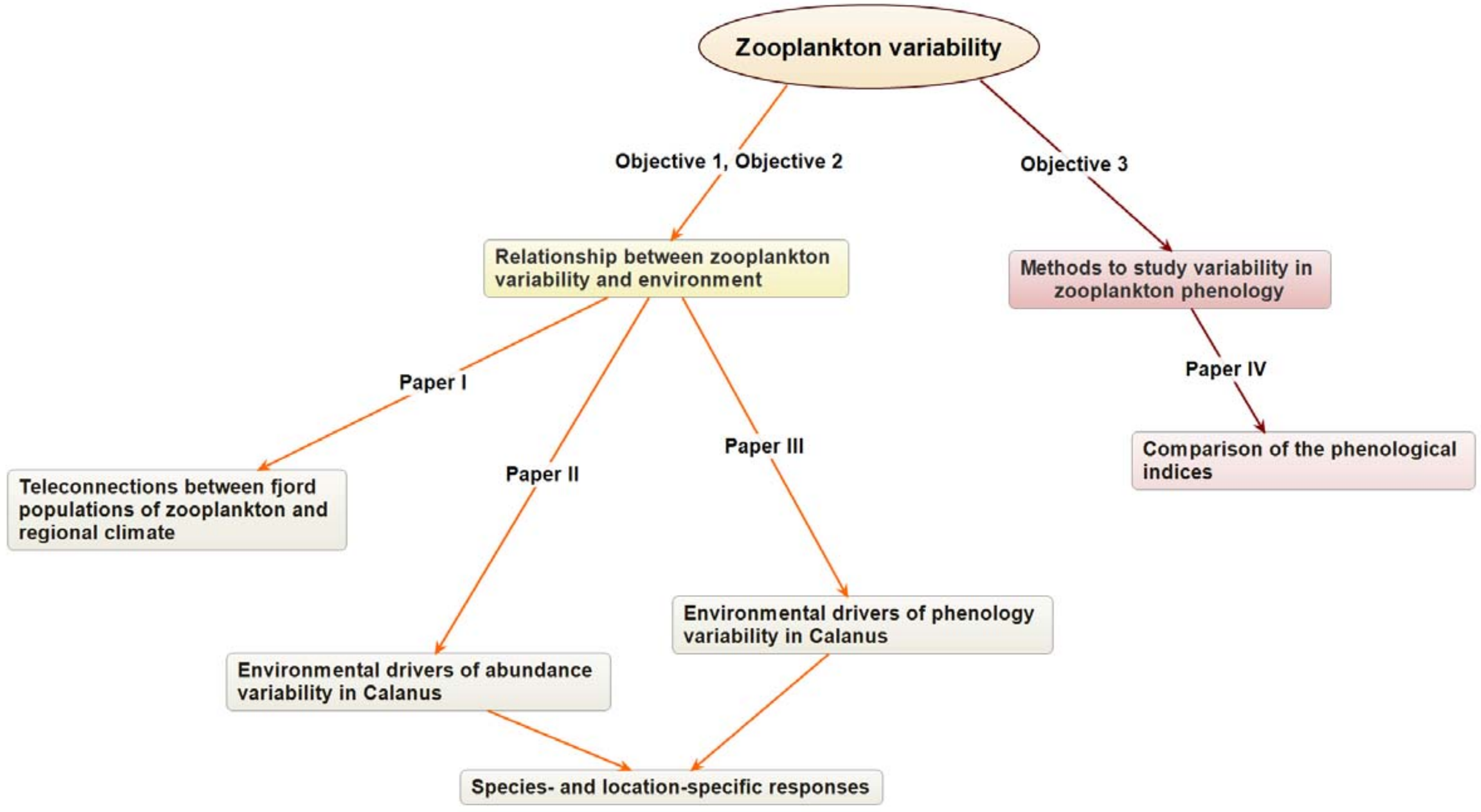


Figure 5. The main structure and topics discussed in this Thesis.

3. Results and Discussion

3.1 Main findings of the Thesis

This Thesis sheds new light on the main drivers of the variability in key North Atlantic zooplankton species and demonstrates that phenological variability can be inferred from data of relatively limited seasonal coverage. The main findings of the Thesis can be summarised as follows:

1) The teleconnections between zooplankton populations and regional climate are likely mediated by the effect of climate variability on local environments such as hydrography, wind regime, precipitation rate, and the resulting effects on primary production and advection of water masses and fauna (**Paper I**).
2) Abundance variability in *Calanus* spp. in the North-East Atlantic is related to both local and large-scale environmental factors, but the responses are location- and species-specific (**Paper II**). Temperature appears to be the main driver of phenology in *Calanus* spp. populations in the North-East Atlantic, while the effects of climate are less clear (**Paper III**).
3) The variability of *Calanus* phenology can be studied using phenological estimates which are based on data of short temporal coverage. The selection of phenological indices is mainly constrained by the season of data sampling and the length of the life cycle of the species (**Paper IV**).

3.2 Long-term variability in overwintering fjord populations of zooplankton

Norwegian fjords represent unique locations to study marine fauna (Brattegard et al., 2011). Fjords populations of zooplankton may to some extent be isolated from the populations that have larger distributions across the North Atlantic but use fjords as temporary habitats for overwintering (Bucklin et al., 2000, Kaartvedt, 1993).

The findings from **Paper I** indicate that the variability in temporary and resident fjord populations are affected by environmental factors acting on a basin-scale. On the other hand, fjord populations are also exposed to more local environmental processes such as upwelling, freshwater runoff, coast-originated winds as well as anthropogenic impacts from coastal industries (Aksnes et al., 2009, Skjoldal and Mare, 1995). **Paper I** demonstrates that the interplay between local and large-scale environmental forcing on fjord zooplankton abundances is likely affected by the topography of fjord basins.

One of the main topographic characteristics of fjords is the depth of the sill (Gade and Edwards, 1980). Fjords with deeper sills tend to have relatively more exchange of water and biota with the surrounding open ocean (Skjoldal, 1995). This water exchange is an important mechanism for mediating the effects of regional environmental factors to zooplankton abundance variability (Syvitski and Shaw, 1995; **Paper I**).

The Norwegian coastal current (NCC) contributes substantially to the water exchange between fjords and the open ocean and advects zooplankton northwards along the Norwegian coast. During late summer, the mixed layer depth of the NCC deepens. This causes the velocity vector of the current to turn landward (Haakstad, 1979, Haakstad, 1977). As a result, advection of zooplankton into fjords is often higher in late summer compared to that in other seasons. Similarly, easterly winds may induce upwelling of deep waters in Norwegian coastal areas and increase inflow of Atlantic water and associated biota into fjords' basins (Skreslet and Loeng, 1977).

Advection and primary production are in turn related to regional climate indices, such as the North Atlantic Oscillation (NAO). NAO in a positive phase induces precipitation during spring and summer and strengthens westerly winds (Hurrell and Deser, 2009). Higher precipitation increases fresh water run-off to fjords, which in turn promote primary production (Tollan, 1976), and thus, zooplankton abundnaces. On the other hand, westerly winds may increase on-shelf transport of Atlantic surface waters and zooplankton to coastal waters and fjords (Sundby, 2000).

Climate – zooplankton connections occur in both shallow- and deep-silled fjords. However, the variation of zooplankton abundance in shallow-silled fjords appears to, take relatively longer time, because water exchange through a shallow sill is limited, and NAO signal from the open Norwegian Sea and coast builds up more slowly in such fjords. In deep-silled fjords, however, zooplankton abundances vary on a shorter time-scale, due to a more frequent exchange of water with the open sea (**Paper I**).

Therefore, two mechanisms are important for the dynamics of fjord populations of zooplankton – the effects of local environmental factors and the effects of large-scale climate that are mediated by the topography-driven water exchange between fjords and open ocean.

3.3 The responses of *Calanus* abundance and phenology to environmental variability

Responses of *Calanus* populations to environmental variability differ across the North Atlantic (Carstensen et al., 2012, Chust et al., 2013). In general, the Arctic species *C. hyperboreus* and *C. glacialis* respond less to environmental variations, especially to climate variability, than do *C. fimarchicus* (Paper II, Usov et al 2013). However, the underplaying mechanisms of these differences remain little understood. Factors that are suggested to affect a population's response to environmental drivers include the location of the population relative to the main distributional range of the species, life-history strategies, the specific sensitivity of developmental stages of the species, and the level of genetic and ecological plasticity in the population under study (Beaugrand, 2011, Smolina et al., 2015, Henriksen et al., 2012).

The results of **Papers I** and **II** indicate that *C. hyperboreus* show fewer responses to local environmental factors than its congeners. This is likely because *C. hyperboreus* was present only in low and unstable abundances compared to that of *C. finmarchicus* in the study locations. The Greenland Sea is the main area of *C. hyperboreus* distribution (Hirche, 1997), thus, *C. hyperboreus* usually sustains only minor local populations in the other areas of the North-East Atlantic (Hirche, 1991). Such fringe populations may inhabit border areas of their ecological niche (Hutchinson, 1957), and thus, may have different sensitivity to local environments than in the core distributional areas

(Beaugrand et al., 2013). Comparing responses to environment in the main distributional area with responses in expatriated populations may, therefore, provide a better understanding of the species-environment relationship on a larger spatial scales.

The relatively weak relationship between *C. hyperboreus* and large-scale climate variability (**Paper I**, **Paper II**) can be attributed to the longer life cycle of *C. hyperboreus*, which is at least 2 years (Hirche, 1997). Thus, total abundance may contain mixed year-classess of *C. hyperboreus*, which integrate climate signals over several years (**Paper II**). Consequently, for poolled abundances, climate effects on year-classes may remain undetected. Therefore, more responses may be found by using each-year's cohort as a correlate of climate.

Developmental stages of *Calanus* spp. are differently affected by environmental factors (Persson et al., 2012, Turner et al., 2006). Results from **Paper II** show that early copepodites of *C. hyperboreus* were inversely related to the Arctic Oscillation index (AO). This was likely due to the negative effect of elevated temperatures during high AO on the development of young copepodites of *C. hyperboreus* (Henriksen et al., 2012; **Paper II**). The older, overwintering stages of *C. hyperboreus* are distributed in deeper waters (Conover, 1988), thus, were little affected by the temperature in surface layers. Climate-driven fluctuations in surface temperature, therefore, were of little importance for older copepodite stages (**Paper II**).

In the White Sea, *C. glacialis* also responded only weakly to climate variability (**Paper IV**; Usov, pers com). One reason for this may be that the White Sea is less affected by hydrographic effects of NAO such as the inflow of Atlantic water masses (Visbeck et al., 2013). In addition, the two-year life cycle of *C. glacialis* in the White Sea (Koosobokova et al. 1999) and resultant mixing of generations in a data analysis, may have prevented the detection of *C. glacialis* responses to climate variability in this location as demonstrated for *C. hyperboreus* in the North-East Atlantic (**Paper II**).

In Svalbard, *C. finmarchicus* abundances did not respond to regional climate, but showed responses to local environmental factors such as temperature, salinity, and spring bloom start (**Paper II**). Interestingly, *C. finmarchicus* phenology in the same location responded to both climate and local temperature (**Paper III**), indicating that phenological responses can be different from responses of total abundance. This further corroborates the idea that *Calanus* responses to environment may differ between developmental stages (**Paper II**).

Experimental research suggests that genetic plasticity to temperature increase is higher in *C. finmarchicus* than that in *C. glacialis* (Smolina et al. 2015). This indicates that *C. finmarchicus* has a potential to increase its distribution in the North Atlantic if climate warming continues as predicted by IPCC (Kjellerup et al., 2012; IPCC, 2014). *C. glacialis*, on the other hand, has a higher ecological plasticity than its congeners, which may imply that *C. glacialis* is capable of phenological shifts and of adjusting reproduction strategy under changing environmental conditions (Daase et al., 2013, Soreide et al., 2016, in prep.). Thus, more knowledge on the significance of both genetic and ecological plasticity of *Calanus* spp. is needed to predict future distribution of *Calanus* spp. in a warmer North Atlantic (Wilson et al., 2015, Smolina et al., 2016, Hinder et al., 2014).

In conclusion, Papers II and III show that both interannual abundance and phenology variability in *Calanus* spp. populations in the North-East Atlantic respond to local environment, but the responses to regional climate are less direct. Responses of *Calanus* variability to both local and large-scale environmental factors vary with the location of the population in the distributional area and with the developmental stages of the species.

3.4 Vertical life table approach to study zooplankton phenology

Part of the study of zooplankton population dynamics is devoted to phenological variability and the relationship between environment and phenology (e.g., Hays et al. 2005, Head 2013). This is usually done by the use of phenological proxies, or indices, of the state of the seasonal development of the population (Ji et al., 2010a, Batten et al., 2009). Phenological indices are typically based on temporal variability in stage-specific or total abundance (Mackas et al, 2012). Common phenology indices applied in studies of zooplankton populations include: the abundance of stage CV (Batten and Mackas, 2009), the cumulative percentile of abundance over a year (Greve et al., 2001), the timing of the central tendency of the total abundance over a year (Edwards and Richardson, 2004), and the appearance of the first copepodite stage (Usov et al., 2013). Such indices are based on stage-resolved abundance data with relatively fine temporal coverage that allow for tracking seasonal variability in the population. This approach is often referred to as a horizontal life table approach (horizontal indices; Aksnes and Ohman, 1996).

An alternative approach is a so called vertical life table approach, which is based on stage-resolved abundance data collected over a relatively short time interval (Aksnes et al., 1997, Aksnes and Ohman, 1996). This approach has been used to estimate vital rates of *Calanus* spp. in the North Atlantic (e.g., Bagøien et al., 2001, Melle et al., 2014, Plourde et al., 2009, Gislason et al., 2007). However, comparatively few studies have applied this approach for phenology in *Calanus* spp. (but see Head et al., 2013).

In Paper IV, I used phenology indices developed by a vertical life table approach (vertical indices) to investigate phenological variability in *Calanus* spp. populations and to study how *Calanus* phenology responds to environmental variability. I used several indices designed to target potential phenological effects occurring both at different stages of *Calanus* development as well as in the population as a whole.

However, it remains unclear to what extent indices based on a vertical life table approach correspond to horizontal indices. **Paper IV** indicated that vertical indices generally correlated with at least one of the horizontal indices of phenology. Moreover, vertical indices showed more correlations with environmental factors than horizontal indices for the same population of *Calanus* (**Paper IV**). This shows that application of phenological indices based on fragmented, season-limited data sets, can provide useful information on phenological variability of zooplankton and environment-phenology relationship.

However, some limitations of the vertical life table approach to zooplankton phenology were revealed (**Paper IV**). Firstly, vertical phenological indices are likely to have limited applicability during the overwintering season of *Calanus* spp., when stage-structure vary little and thus, is likely to be less responsive to environmental forcing (**Paper II**, **Paper IV**). Secondly, some phenological indices may have limited applicability for species with a multi-annual life cycle. In this case, older copepodite stages from consecutive cohorts may sometimes overlap in the population. This may distort the estimates of the vertical phenological indices based on abundances of older copepodite stages. Thus, care must be taken when this index is used for multi-annual zooplankton species. Lastly, indices that are based on either early or late copepodites stages, cannot be used in seasons, when the abundance of respectively, early or late copepodites is minimal (**Paper III**, **Paper IV**).

These results show that with the application of vertical phenological indices, studies of *Calanus* and other zooplankton species abundances that are based on seasonally-limited data (e.g., Gislason et al., 2014b, Kwasniewski et al., 2013, Daase et al., 2007) can be accompanied by the analysis of phenological responses of the same populations to environment. This, more integrated approach to study zooplankton variability, may contribute to new knowledge on the dynamics of zooplankton populations (Richardson and Shoeman 2004).

4 Conclusions

The findings of this Thesis expand the knowledge on the dynamics of zooplankton populations by identifying main environmental factors contributing to zooplankton abundance variability in the North-East Atlantic and studying some mechanisms behind zooplankton-environment relationship. In essence, this work highlights that the relationship between zooplankton and environment vary with the topography of the habitat and advection of water masses, but also with location relative to the core distributional area and with the developmental stage of the species. This work suggests that studies of phenology can be an alternative approach to detect environmental effects on zooplankton populations, also when temporal coverage of data is limited. Thus, the results of this Thesis contribute to enhancing the understanding of the dynamics of marine pelagic ecosystems and to facilitating the assessment of environmental impacts on these ecosystems.

5. Outlook for future research

The analysis of zooplankton time-series provided here, was limited by the length of the study period (mainly 15 – 22 years). Some zooplankton populations respond to environmental factors only after several a years time-lag. Therefore, environmental effects are more likely to be observed in a longer data series (Conversi et al., 2001, Greene and Pershing, 2000), and data spanning several decades ensure a more accurate analysis of zooplankton variation and its relationship with the environment (Stenseth et al., 2004).

Although vertical phenological indices were shown to be a reliable method to analyse zooplankton phenology variation (**Paper IV**), more data covering the whole life cycle of zooplankton species is needed. In particular, in the sub-Arctic and Arctic locations, the availability of such data is limited. This impedes an analysis of year-round variability in phenology in these locations. Data-series covering the whole life cycle of key zooplankton species in these areas would be useful to further develop methodology for phenological studies. In addition, phenological studies will be even more advanced by using data which includes both copepodite and naupliar and life stages (Eiane and Ohman, 2004).

Comparatively few studies so far have focused on fjord populations of zooplankton (e.g., Eiane et al., 2002, Bagøien et al., 2001). Based on the results of this Thesis, I suggest that fjord pelagic communities should be studied more closely. There is still insufficient understanding of what is the degree of isolation of fjord populations from the open ocean populations (Niehoff and Hirche, 2005, Weydmann et al., 2016). Question that needs more investigation is whether fjord populations have the same ecological and genetic adaptations as the open ocean populations. Moreover, the mechanisms that are responsible for water exchange between fjords and open ocean and its effects on fjord populations of zooplankton have been studied only in a few locations along the Norwegian coast (Basedow et al., 2004, Skjoldal, 1995), but can also be investigated in the other fjords. This will further increase the knowledge on zooplankton variability in coastal ecosystems.

Of the research that has been devoted to comparisons of data-series of *Calanus* and other key zooplankton species in the North Atlantic (Gislason et al., 2014a, Head et al., 2013, Daase et al., 2013), only a few addressed within or between-basins comparison of zooplankton (Unal and Bucklin, 2010, Chiba et al., 2015, Greene et al., 2003). I propose that more comparisons of zooplankton time-series between oceanic basins are made. Such comparisons will help to measure synchronicity between zooplankton populations at a large-scale and to identify how this synchronicity changes with distance between the populations (Koenig, 2002, Ripa, 2000, Ranta et al., 1999).

In this Thesis, the role of predation on zooplankton variability was generally not discussed. However, predation exerts a strong effect on zooplankton abundance variability in the North-East Atlantic (Dalpadado and Mowbray, 2013, Huse and Toresen, 1996, Stige et al., 2014). Predation causes mortality of both early and late developmental stages of zooplankton, thus, the effects of predation on zooplankton can be complicated (Eiane et al., 2002, Ohman and Hirche, 2001, Plourde et al., 2009). Predation seems also to influence life-strategy decisions for their key zooplankton prey, such trade-offs between duration of feeding in surface waters and the timing of retreat to greater depths (Varpe et al., 2007). Such decisions likely affect phenology of zooplankton. Therefore, predator seasonality and abundance should be accounted for in studies of variability in zooplankton populations. This is also useful to understand how relative timing of zooplankton and its predators would be affected if the phenology of both trophic groups changes in response to environmental variability (Durant et al., 2007, Orlova et al., 2015).

Paper II

Polar Biol
DOI 10.1007/s00300-017-2150-z

ORIGINAL PAPER

The role of local and regional environmental factors for *Calanus finmarchicus* and *C. hyperboreus* abundances in the Nordic Seas

Marina Espinasse[1] · **Claudia Halsband**[2] · **Øystein Varpe**[2,3] · **Astthor Gislason**[4] · **Kristinn Gudmundsson**[4] · **Stig Falk-Petersen**[2,5] · **Ketil Eiane**[1]

Received: 21 July 2016 / Revised: 31 March 2017 / Accepted: 19 June 2017

Abstract In the advective realm of the seas, it is challenging to disentangle the role of regional and local processes on zooplankton populations. However, comparative studies of spatially separated zooplankton populations can provide valuable insights into this issue. We studied interannual abundance variation of the key zooplankton species *Calanus finmarchicus* and *C. hyperboreus* in three near-shore locations of the Nordic Seas: off northern Norway, Svalbard, and northern Iceland. Average abundances of both species were similar among locations, while in each location the abundance of *C. finmarchicus* was about an order of magnitude higher than the abundance of *C. hyperboreus*. The abundance of both species decreased in northern Norway, while *C. finmarchicus* abundance increased in northern Iceland. *C. finmarchicus* abundance in northern Norway covaried with regional climate, while the Svalbard *Calanus* populations were related to local environment (hydrography, phytoplankton). In northern Iceland, *C. finmarchicus* abundance covaried with local environmental factors, while *C. hyperboreus* abundance covaried with climate variability. Top-down forcing could not be investigated. The results indicate that the mechanisms relating regional climate variability (North Atlantic and Arctic oscillations) to *Calanus* abundance are mediated through advection of water masses, while more local environmental variability involved bottom-up processes or advection.

Keywords Abundance variation · *Calanus* · Climate variability · Spatial ecology · Sub-Arctic Atlantic

Introduction

Environmental variability is an important driver of abundance in marine zooplankton, but the relationships between zooplankton dynamics and local as well as regional environmental factors are often poorly understood (Beaugrand 2012). The analyses of abundance patterns over time can provide insight into the underlying mechanisms that determine abundance fluctuations in zooplankton at large geographical scales (Perry et al. 2004; Mackas and Beaugrand 2010) and at local scales (Eloire et al. 2010). Such analyses are, however, rare, especially for populations in remote and inaccessible regions.

In the Nordic Seas, the genus *Calanus* is one of the most ecologically important zooplankton taxa (Melle et al. 2004; Wassmann et al. 2006). The congeneric species *Calanus finmarchicus*, *C. glacialis*, and *C. hyperboreus* represent a main food source for many planktivores, including economically important species such as capelin (Falk-Petersen et al. 1986), cod (Ellertsen et al. 1987), and herring (Dalpadado et al. 2000; Varpe et al. 2005). *Calanus* spp. have different reproductive strategies and generation times. *C finmarchicus* usually has a one-year generation time and reproduces in surface waters when sufficient food is

✉ Marina Espinasse
marina.chelak@nord.no; ecologM@hotmail.com

[1] Faculty of Bioscience and Aquaculture, Nord University, P.O. Box 1490, 8049 Bodø, Norway

[2] Akvaplan-niva, Fram Centre, P.O. Box 6606, Langnes, 9296 Tromsø, Norway

[3] The University Centre in Svalbard (UNIS), P.O. Box 156, 9171 Longyearbyen, Norway

[4] Marine and Freshwater Research Institute, P.O. Box 1390, Skulagata 4, 121 Reykjavik, Iceland

[5] Norwegian Polar Institute, Fram Centre, P.O. Box 6606, Langnes, N-9296 Tromsø, Norway

present, often in spring (Melle and Skjoldal 1998; Niehoff et al. 2000). *Calanus glacialis* has a life cycle of 1–3 years and is capable of boosting reproduction from lipid reserves before the start of the bloom, but sometimes starts reproduction in the presence of other food sources (Falk-Petersen et al. 2009; Daase et al. 2013). In contrast, the generation time of *C. hyperboreus* is 2–5 years, and eggs are produced deep in the water column, based on reserves in the absence of food (Hirche and Niehoff 1996; Halvorsen 2015). Although the ecology of the *Calanus* spp., and *C. finmarchicus* in particular, is fairly well described (Tande and Miller 2000), better understanding of their long-term abundance fluctuations is needed for any predictions of marine ecosystem change in the northernmost areas of the North Atlantic (Villarino et al. 2015).

Large-scale changes in the distribution of these *Calanus* spp. occurred in response to climate change, as evident from the shifts of their distributions (Beaugrand et al. 2002; Chust et al. 2013). The hydroclimatic regime of the northern hemisphere is influenced by changes in the atmospheric climate, characterized by the North Atlantic Oscillation index (NAO) and the Arctic Oscillation index (AO). These climatic oscillations have been shown to covary with zooplankton abundances in the North Atlantic via their effect on advection (Greene and Pershing 2000), primary production (Skreslet et al. 2015), or an interaction of physical and biological factors (Fromentin and Planque 1996; Planque and Taylor 1998). If such regional and more local environmental factors exhibit similar patterns across large distances, the Moran effect can be observed (Koenig et al. 2002), when environmental factors provide similar effects on the distinct zooplankton populations and thus cause synchrony in the zooplankton population dynamics (Lodi et al.; Batchelder et al. 2012).

For example, the increase in sea surface temperature in the Barents Sea (Wassmann et al. 2011), the Norwegian Sea (Walczowski et al. 2012), and in the Arctic Ocean (Steele et al. 2008) may shift the North Atlantic *Calanus* community to a state characterized by more boreal and fewer arctic species (Carstensen et al. 2012; Kjellerup et al. 2012). As the smaller, boreal *C. finmarchicus* provides less nutritional value per individual than its Arctic congeners *C. glacialis* and *C. hyperboreus*, such shifts may reduce energy flows to higher trophic level organisms in the Arctic (Falk-Petersen et al. 2007; Karnovsky et al. 2010). Alternatively, the responses of *Calanus* abundance to regional forcing may not be uniform across the North Atlantic, if the local manifestations of the hydroclimatic variations differ between locations (Planque et al. 1997; Drinkwater et al. 2013), e.g. in terms of advection of water masses (Sundby 2000; Hansen et al. 2012), changes in temperature, or the timing of the spring bloom (Fromentin and Planque 1996). In parts of the western North Atlantic, *C. finmarchicus* abundance is positively related to NAO (Greene et al. 2003), while the correlation is negative in the eastern North Atlantic (Planque and Taylor 1998). Also, congeneric populations and distinct life-cycle stages of *Calanus* may vary in their responses to climate variability (Turner et al. 2006) and water temperature (Persson et al. 2012).

Here, we study abundance variation of *C. finmarchicus* and *C. hyperboreus*, by utilizing long-term data series from three locations of the Nordic Seas: northern Norway, Svalbard, and northern Iceland. We aim to identify and discern (1) long-term abundance trends, (2) common regional drivers affecting populations across the basin, and (3) specific local conditions driving *Calanus* populations in these locations.

Materials and methods

Study areas

We focus on the Nordic Seas region of the North Atlantic Ocean (Fig. 1). The oceanic circulation in the Nordic Seas is influenced by the inflow of Atlantic water (Hansen and Østerhus 2000). A main source of Atlantic water is the Norwegian Atlantic Current (NAC, Fig. 1). The NAC flows along the shelf break off western and northern Norway and bifurcates with one branch entering the Barents Sea and the other flowing northwards along the western coast of Svalbard as the West Spitsbergen Current (WSC, Fig. 1) (Sætre et al. 2004; Blindheim and Østerhus 2005). Northwest of Svalbard the WSC splits, and one branch enters the Arctic Ocean, while the other branch is deflected southwards along the east coast of Greenland and enters the Iceland Sea parallel to the East Greenland Current (EGC, Fig. 1) (Blindheim and Østerhus 2005). The EGC transports cold and Arctic water masses to the Iceland Sea, while the North Icelandic Irminger Current (NIIC, Fig. 1) supplies warmer Atlantic waters to the area north of Iceland. The East Icelandic Current (EIC) brings Arctic water masses eastwards along the North Icelandic continental slope (Valdimarsson and Malmberg 2003). Together with the EGC, the EIC forms a strong temperature gradient where it meets the warm Atlantic waters of the NIIC (Valdimarsson and Malmberg 1999). The Faroe current (FC; Fig. 1) enters the Nordic Seas between Iceland and the Faroe Islands and supplies Atlantic Water to the southwest part of the Norwegian Sea. The whole circulation cycle in the Nordic Seas is suggested to take around 15 years (Aksnes and Blindheim 1996; Blindheim and Østerhus 2005).

Calanus finmarchicus and *C. hyperboreus* abundance data

Three areas of the Nordic Seas are considered in the study: northern Norway in the east, western Svalbard shelf in the

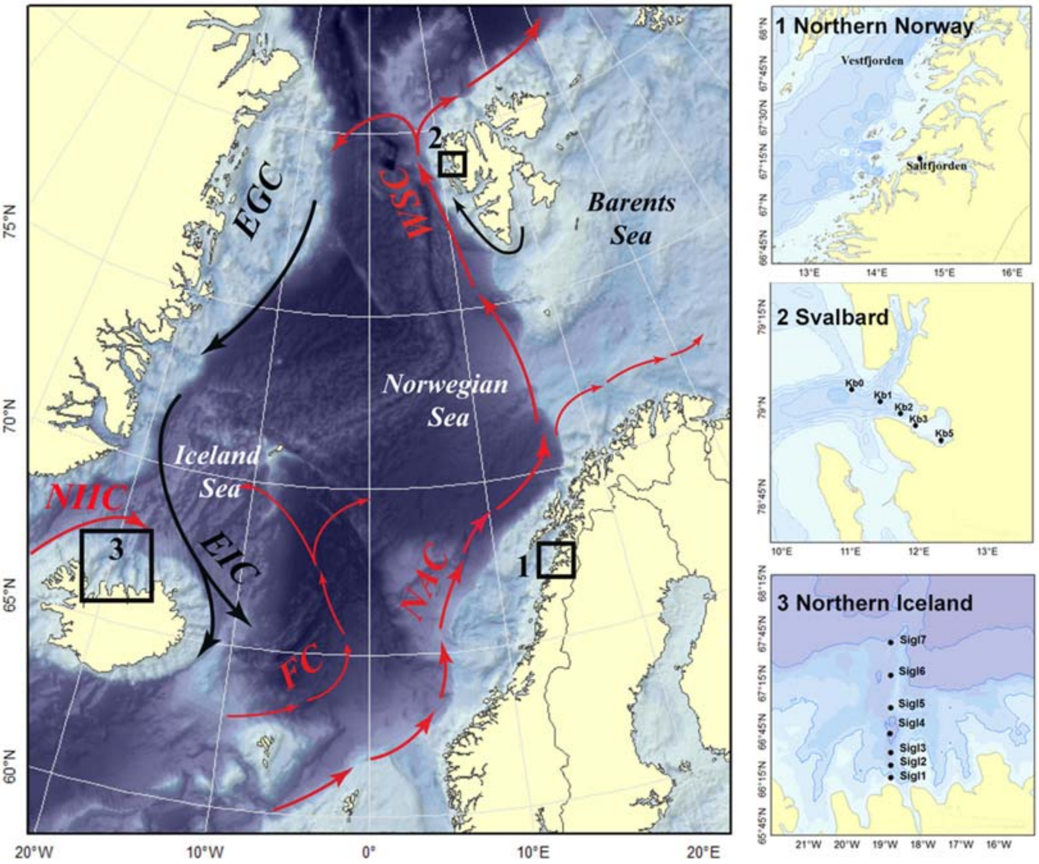


Fig. 1 Map of the study area with sampling locations and main oceanic circulation, based on Loeng and Drinkwater (2007) and Drinkwater et al. (2013). *1* a fjord station in northern Norway; *2* a transect on the west coast of Svalbard; *3* a transect in the northern Icelandic waters. The codes for indicated currents are *FC* Faroe current, *NIIC* North Icelandic Irminger current, *NAC* Norwegian Atlantic current, *WSC* West Spitsbergen current, *EGC* East Greenland current, and *EIC* East Icelandic current. *Red and black arrows* denote warm and cold water currents, respectively

north, and the northern Icelandic shelf in the west (Fig. 1). This allows large spatial coverage from three similar but well-separated near-shore locations. Importantly, however, the sampling at the three locations took place at different times of a year (October, July, and May, respectively), and the sampling design (sampling depth and equipment) differed slightly between the locations. These differences could lead to variation in the abundance and composition of the developmental stages between the locations. However, to the best of our ability, we take these differences into account when comparing the variation of the species abundances between the locations. We focus on identifying the specific responses of *Calanus* in relation to the location and time of sampling, and when interpreting these responses, we seek to describe location-specific mechanisms. Thus, although different times of sampling complicate some of the interpretations, the cost of losing information due to different sampling times in return improves spatial coverage of the study and allows for between-location comparisons.

In northern Norway, zooplankton was sampled at a fixed station in Saltfjorden (67.15°N, 14.38°E; Fig. 1) in October from 1983 to 2010 (except in 1985) (Table 1). Five replicate hauls were taken with a Juday net (0.1 m^2 aperture and 180 μm mesh size) from near the seabed at 370 m depth to the surface.

Kongsfjorden (79°N, 12°E; Fig. 1) is a glacial fjord located on the west coast of the Svalbard archipelago.

Table 1 Overview of the data series from northern Norway, Svalbard, and northern Iceland, used in this study

Location and stations	Sampling gear	Sampling depth (m)	Year and season	Total number of samples
Northern Norway, Saltfjorden	Juday net (180 µm)	0–370	October, 1983–2010	133
Svalbard				
KB0	Multinet (180 µm)	315–200–100–50–20–0	July, 1996–2010	63
KB1		352–200–100–50–20–0		
KB2		330–200–100–50–20–0		
KB3		329–200–100–50–20–0		
KB5		96–50–20–0		
Northern Iceland, Siglunes (Sigl) 1–7	WP2 net (200 µm)	0–50	May, 1990–2011	152

Zooplankton samples were collected in July at five stations from 1996 to 2010, but not 1998 and 2005 (Table 1; Fig. 1), by vertical hauls of a Multinet (Hydrobios ltd.; 0.25 m^2 aperture and 180 µm mesh size). Station KB0 was not sampled in 1996 and station KB5 was not sampled in 2007. Samples were collected from near the seabed at maximal 352 m depth to the surface in five depth bins.

Data from northern Iceland were collected along a transect of seven stations extending from the coast to the Iceland Sea (67°N, 18°50′; Fig. 1) in May from 1990 to 2011 (Gislason et al. 2014). Station Sigl 1 was not sampled in 2000 and station Sigl 6 was not sampled in 2007 (Fig. 1; Table 1). In 1990 and 1991, a Hensen plankton net (0.42 m^2 mouth area and 200 µm mesh size) was used. All subsequent sampling was conducted with a WP2 net (0.25 m^2 aperture and 200 µm mesh size). Both Hensen and WP2 nets were towed from 50 m to the surface. The sampling depth in northern Iceland was much shallower than in northern Norway and Svalbard. However, most of *Calanus* individuals at this time of a year (May) in northern Iceland reside in surface areas for spawning and feeding (Gislason and Silva 2012), and thus, the potential underestimation was likely minor.

Sample treatment and abundance calculations were equivalent in all regions. The zooplankton samples were preserved in a 4% formaldehyde–seawater solution until enumeration in the lab. *C finmarchicus* was staged (copepodite developmental stages CI–CVI) in all samples, while only total abundance of *C. hyperboreus* was counted for northern Norway. Species separation of *Calanus* was done from randomly selected subsamples based on prosome length distributions (Unstad and Tande 1991; Hirche et al. 1994). Abundance estimates (ind m^{-2}) were calculated assuming 100% filtering efficiency of the net, except for WP2 nets in northern Iceland, where filtered water volume was measured with a flowmeter (Hidrobios ltd.) fitted in the mouth of the net.

Morphological criteria are not always a reliable taxonomical tool and may lead to misidentification between *C. finmarchicus* and *C. glacialis,* as shown by molecular identification methods (Lindeque et al. 2006; Gabrielsen et al. 2012). According to Skreslet et al. (2015), the number of *C. glacialis* misidentified as *C. finmarchicus* in northern Norway was about 5%, and in Svalbard, misidentification could be up to 20% (Gabrielsen et al. 2012), while such estimates are not available for northern Iceland.

Environmental variables

We distinguish between local and regional environmental variables. We consider those environmental variables that vary on the spatial scale of sampling (such as hydrographic variables) as primarily local variables, while those varying on a regional (e.g. North Atlantic) scale, such as climate indices, as large-scale environmental variables. Local-scale environmental variables are temperature, salinity, and chlorophyll *a* (Chl *a*), and were measured as follows: before 1991, water temperature in Northern Norway was measured with calibrated reversing thermometers fitted to Nansen bottles, and salinity was measured in the lab from water samples with a salinometer. From 1991 onwards, salinity and temperature were measured with a conductivity, density, and temperature (CTD) profiler (either Sea-Bird Electronics or Sensordata). In Svalbard and northern Iceland, a CTD cast (Sea-Bird Electronics) at each sampling station obtained salinity and temperature profiles. In situ Chl *a* concentrations are available for northern Iceland only and were estimated by filtering 1 or 2 L water samples collected at 10 and 30 m depth onto GF/C glass fibre filters that were subsequently analysed by a spectrophotometer as described in UNESCO/SCOR (1996). For all locations, depth-averaged (0–50 m) hydrographic data were used for analyses.

The degree of overlap between timing of the phytoplankton spring bloom and the occurrence of early developmental stages can be an important factor for copepod recruitment (Diel and Tande 1992; Melle and Skjoldal 1998; Søreide et al. 2010). To study relationships between

Calanus abundance and year-to-year variability in the timing of the spring bloom, we estimated the start date of the yearly spring blooms based on remote sensing data on changes in Chl *a* concentration in the vicinity of our study locations. We used data collected by NASA (SeaWifs and Aqua-MODIS) and ESA (MERIS) available from the Hermes portal of the European Service of Ocean Colour (http://hermes.acri.fr/index.php?class=archive). The downloaded Chl *a* levels are measurements from 8-day intervals from site-specific areas of approximately 4.63 × 4.63 km merged by a Garver, Siegel, and Maritorena model (GSM) (Maritorena and Siegel 2005; Maritorena et al. 2010). To avoid distortion caused by terrestrial interference for the locations in northern Norway and Svalbard, measurements were taken from rectangular areas outside the fjords (from 67°10′N to 67°37′N and 12°30′W to 14°15′W; and 78°45′N to 79°14′N and 9°30′ to 11°, respectively). For northern Iceland, remote Chl *a* measurements were extracted from a rectangular area enclosing the transect (from 66°30′N to 67°45′N and from 17°30′W to 19°15′W). The satellite Chl *a* levels were extracted and processed in R (R Core Team 2016). A linear interpolation with respect to day numbers between recorded concentrations of Chl *a* from the selected areas was performed for the years 1998–2010 (until 2011 for northern Iceland). The spring bloom start was estimated as the day number when Chl *a* concentration exceeded 5% above the median Chl *a* concentration for that year and location (Siegel et al. 2002; Henson et al. 2009).

As proxies for the regional climate variability, we used the North Atlantic Oscillation index (NAO; http://www.climatedataguide.ucar.edu) and the Arctic Oscillation index (AO; http://www.cpc.noaa.gov/) (Hurrell 1995; Cohen and Barlow 2005). NAO describes the difference in normalized atmospheric pressure between the Azores and Iceland. This is seen as the main mode of interannual variability of atmospheric circulation in the North Atlantic (Hurrell 1995; Hurrell et al. 2001) and affects marine ecosystems through the regulation of wind regime, storminess, and gyre circulation (Hurrell and Deser 2009). AO is a pressure seesaw that has the centre of action in the Arctic and regulates the climate and weather processes at high north latitudes. To assess the effect of large-scale climate on the interannual variation of *Calanus* abundances, we applied average annual indices of NAO and AO.

Data analysis

For each location and year, we calculated average total abundances of *Calanus* and relative composition (%) of copepodite stages of both species over stations in Svalbard and northern Iceland, and for replicates in northern Norway. The data sets of both abundances and environmental factors generally contained outliers and deviated significantly from normality (Shapiro–Wilks normality test); thus, we used a non-parametric, Kendall's rank correlation (Kendall and Gibbons 1990) to test for covariation between environmental variables, between abundances of both *Calanus* spp., and each of the environmental variable, and to detect temporal change (trends) in *Calanus* abundances. All correlation tests were done in R (R Core Team 2016).

Abundance anomalies for overlapping years (1996–2010) for both *Calanus* species were calculated as $\hat{x} = (x - \mu) \times \sigma^{-1}$, where μ is the mean value of x (yearly average abundance) over the selected time window and σ is the corresponding standard deviation.

To describe the relationships between environmental variables and different developmental stages of *Calanus* and to identify environmental variables that significantly explained the interannual variation in stage-specific abundances, we applied a constrained ordination method—Redundancy Analysis (RDA) in Canoco v. 5.0 (ter Braak and Smilauer 2012). This is a linear model and it was preferred to the alternative unimodal model (Canonical Correspondence Analysis, CCA) based on the Detrended Correspondence Analysis (DCA). The DCA showed that the gradient length of the first axis was less than 4 standard deviations, indicating linear responses of both *Calanus* spp. to environmental variability (ter Braak and Smilauer 2012). For the RDA, the abundance data were ln $(x + 1)$ transformed to homogenize variance of the abundances. Temperature, salinity, Chl *a* concentration (for Icelandic data), and annual NAO and AO indices were included in the RDA as explanatory variables. The spring bloom start was not included in the RDA due to limited number of years (14) with data. To account for autocorrelation between stations in the data from Svalbard and northern Iceland, Monte-Carlo permutations (499) were restricted to a split-plot design. Permutations were not performed for the whole-plot factor (stations), but permutations for time-series data dependent across whole-plots were applied for split-plots (years) (ter Braak and Smilauer 2012). As the split-plot design required an equal number of samples each year, we interpolated the values for the missing samples in Svalbard and northern Iceland, using random imputation in R. In analysing data from northern Norway, permutations for time-series data were used in the Monte-Carlo test, as the data were collected annually from one station.

Results

Environmental variability

Average temperatures in the surface layer (0–50 m) were generally higher in northern Norway in autumn than in summer in Svalbard and in spring in northern Iceland (Table 2; Fig. 2). Temperature varied less in northern

Table 2 *Calanus finmarchicus* and *C. hyperboreus* average abundances (ind m^{-2}) and environmental variables in northern Norway in October (1983–2010), in Svalbard in July (1996–2010), and in northern Iceland in May (1990–2011)

Variable (mean)	Northern Norway	Svalbard	Northern Iceland
C. finmarchicus abundance, ind m^{-2} (SD)	44914.2 (27880.2)	50022.9 (37151.9)	37431.1 (54239.1)
C. hyperboreus abundance, ind m^{-2} (SD)	1476.8 (2350.7)	3108.9 (2360.9)	1080.1 (2247.6)
Temperature, °C (SD)	8.99 (0.64)	3.57 (1.25)	3.63 (1.20)
Salinity, psu (SD)	32.17 (0.74)	33.60 (1.10)	34.75 (0.23)
Chl *a* concentration, µg L^{-1} (SD)	NA	NA	5.58 (3.75)
The spring bloom start, day of a year (SD)	121 (4.82)	147 (14.00)	154 (11.92)

Temperature, salinity, and Chl *a* are averages from 0 to 50 m. The spring bloom start is derived from satellite data

SD standard deviation, *NA* data not available

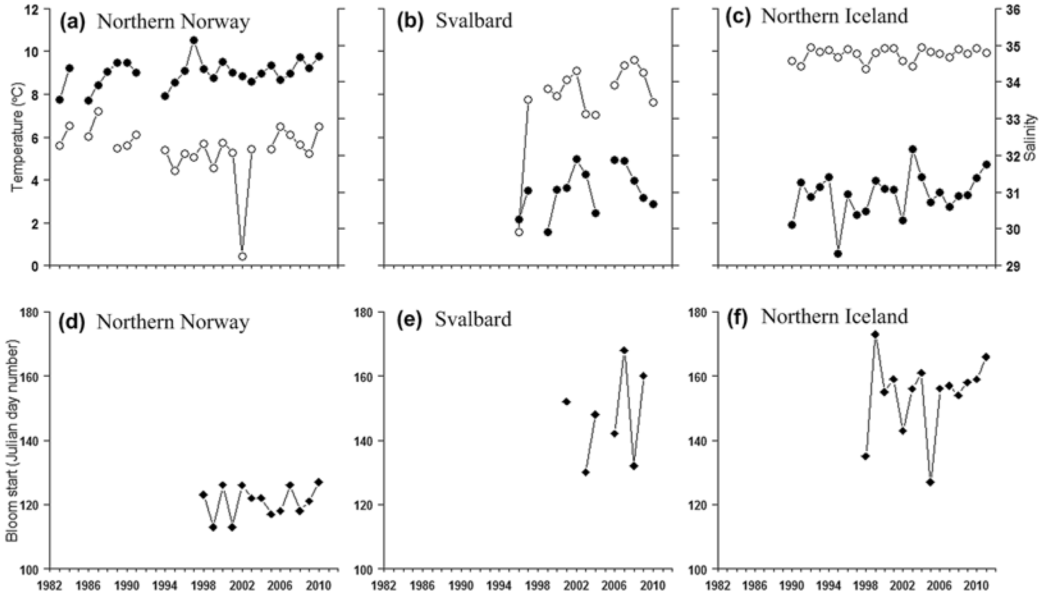


Fig. 2 Averaged temperature (°C, *black circles*) and salinity (*open circles*) in 0–50 m over all stations, and the start day of the spring bloom (day of year; *diamonds*) from northern Norway (**a**, **d**), Svalbard (**b**, **e**), and northern Iceland (**c**, **f**). The start day of the spring bloom was calculated from the remote sensor data on Chl *a* concentration (see text for details)

Norway, whereas in Svalbard and northern Iceland it varied at about the same amplitude. Northern Iceland had the highest average salinities, while in Svalbard waters salinity was intermediate and more variable, and the lowest average salinity was observed in northern Norway (Table 2; Fig. 2).

Averaged Chl *a* concentration recorded in northern Iceland in May was 5.6 µg L^{-1} (Table 2). The average day of the spring bloom start during the investigated period (1998–2010 in northern Norway and Svalbard, and 1998–2011 in northern Iceland) occurred in late April in northern Norway, in late May in Svalbard, and in the beginning of June in northern Iceland (Table 2). We did not detect trends in any of the environmental variables studied.

Both NAO and AO indices were low at the beginning (1985, 1987) and at the end of the study period (2010), and relatively high values occurred in 1986, 1990, and 2011 for NAO, and in 1989 and 1990 for AO (Fig. 3). Low values of NAO and AO coincided with relatively low temperature and salinity values in Svalbard in 2010 (Figs. 2, 3), and positive correlations were found between NAO, AO, and salinity and temperature in Svalbard (Table 4). AO correlated positively with the spring bloom start in northern Iceland (Table 4) and negatively in Svalbard (Table 4).

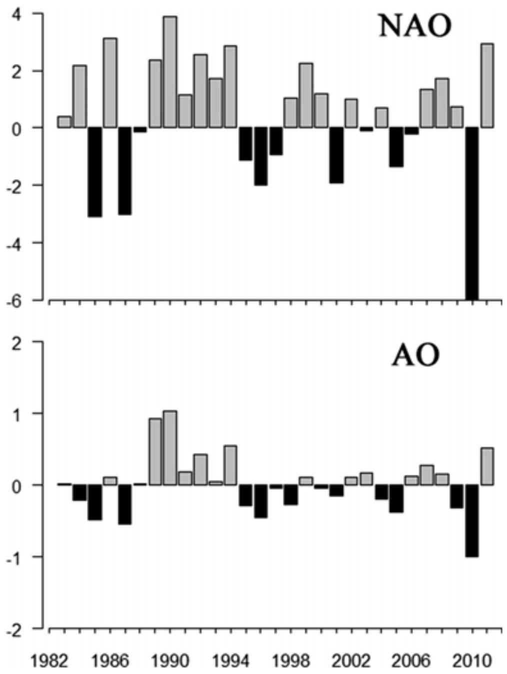


Fig. 3 Annual mean NAO and AO during 1983–2011

Variations of *Calanus* spp. abundances between locations

The average abundances of *C. finmarchicus* in the study locations were fairly similar (Table 2; Fig. 4). *Calanus hyperboreus* abundances were substantially lower than those of *C. finmarchicus* in all three locations (Table 2; Fig. 4). For both *C. finmarchicus* and *C. hyperboreus*, the abundance variability was higher in northern Iceland than in northern Norway and Svalbard (Table 2). The population of *C. finmarchicus* consisted almost exclusively of late copepodite stages IV and V in northern Norway in October (Fig. 5). In contrast, samples in Svalbard and northern Iceland were taken relatively soon after spawning of *C. finmarchicus*, and the stage structure in both locations was more variable, with stages CI–III being abundant (typically accounting for 50–90% of the population). The population of *C. hyperboreus* in Svalbard consisted mainly (ca. 90%) of copepodites stages IV and V, while in northern Iceland young copepodites (CI–CIII) accounted for ca. 66% of total counts (Fig. 5). We have no information on the stage structure of *C. hyperboreus* in northern Norway.

In northern Norway, abundances of *C finmarchicus* and *C. hyperboreus* decreased during the study period, while in northern Iceland, *C. finmarchicus* abundance increased (Table 3). We did not observe temporal change in the abundance of *C. hyperboreus* in northern Iceland and in either species in Svalbard.

For 1996–2010, where we have data for all three study locations, positive and negative abundance anomalies for *C. finmarchicus* were relatively evenly distributed in northern Norway (Fig. 6). In the other populations, however, most years were characterized by negative abundance anomalies. While negative anomalies were largely <1 SD (in absolute values), the relatively few years with positive abundance anomalies were sometimes 2–3 SD above the period mean (Fig. 6). Interestingly, the highest positive anomalies of *C. finmarchicus* and *C. hyperboreus* abundances in northern Iceland in 2005 coincided with the earliest spring bloom start (early May). However, neither species in northern Iceland correlated significantly with the spring bloom start. In Svalbard, the high positive anomalies of *C. finmarchicus* in 2009 and of *C. hyperboreus* in 2001 coincided with delayed spring bloom start (beginning of June), and *C. finmarchicus* abundance correlated positively with the spring bloom start in Svalbard (Table 5).

Correlations between total abundances and environmental factors

In northern Norway, *Calanus* abundances covaried with climate indices only. Abundance of *C. finmarchicus* correlated positively with the yearly mean AO and the yearly mean NAO (Table 5). In Svalbard waters, *C. finmarchicus* correlated positively with both average temperature and salinity in 0–50 m, and the spring bloom start, whereas *C. hyperboreus* correlated positively with temperature. However, temperature and salinity in Svalbard covaried (Table 4). In northern Iceland, *C. finmarchicus* correlated positively with temperature and salinity, but correlated inversely with Chl *a* concentration, while *C. hyperboreus* inversely correlated with NAO. Average temperature and salinity in the upper 50 m were also correlated in northern Iceland (Table 4).

The relationships between stage-specific abundances of *Calanus* and environmental variables (temperature, salinity, annual NAO and AO, and for northern Iceland, Chl *a*; Fig. 7) showed that in Svalbard annual AO contributed significantly ($P = 0.036$) to explaining the interannual variation of the stage-specific abundances of *C. finmarchicus* and *C. hyperboreus*, and accounted for 8.2% of the variation in the abundances of the copepodite stages of the two *Calanus* spp. In northern Iceland, temperature contributed significantly ($P = 0.04$) to explaining the variation of *Calanus* stages' abundances and accounted for 8% of the total variation in the copepodite stages' abundances (Fig. 7). Copepodite stages II and III of *C. hyperboreus* in Svalbard were inversely related to AO anomalies, while other copepodite stages of *C. hyperboreus* and

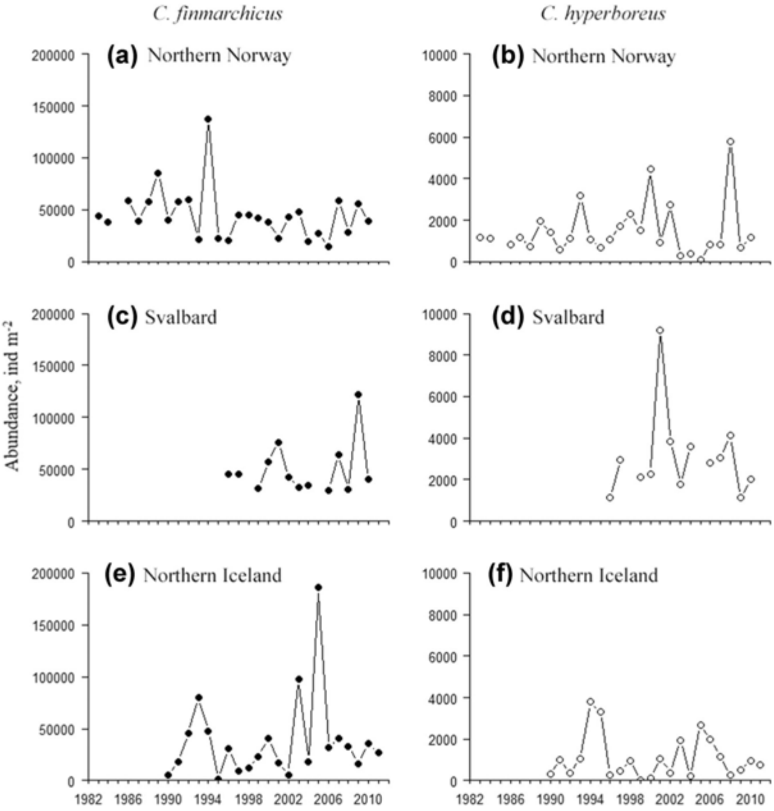


Fig. 4 Average abundance (ind m^{-2}) of *Calanus finmarchicus* (*black circles*) and *C. hyperboreus* (*open circles*) from northern Norway (**a**, **b**), Svalbard (**c**, **d**), and northern Iceland (**e**, **f**)

copepodite stages of *C. finmarchicus* were not related to AO. Early copepodites (CI to CIII) of *C. finmarchicus* showed an association with higher temperatures, while CI of *C. hyperboreus* were found in higher abundances at lower temperatures (Fig. 7). None of the environmental variables contributed significantly to the variation in *Calanus* copepodite abundances in northern Norway.

Discussion

Our results suggest that the dynamics of the studied *Calanus* populations were related to environmental variability driven by both local and regional processes, and these relationships were species—and location—specific.

Effects of regional and local environment on *Calanus*

The abundances of *C. finmarchicus* in northern Norway correlated positively and *C. hyperboreus* in northern Iceland correlated negatively with climate variability (NAO or AO). Skreslet and Borja (2003) and Skreslet et al. (2015) attribute the relationship between NAO and *C. finmarchicus* in northern Norway to high freshwater discharge to coastal waters during periods of high NAO (Hurrell and Deser 2009). Higher freshwater inflow, they hypothesize, tends to increase primary productivity and, as an effect of increased food availability, may elevate the abundance of *C. finmarchicus.*

Positive NAO and AO anomalies are associated with strong westerly winds in the North East Atlantic and thus with an intensified inflow of Atlantic water masses to subpolar regions (Kerr 1999; Dickson et al. 2000; Ottersen et al. 2001). This inflow is associated with advection of Atlantic zooplankton (of which *C. finmarchicus* is a dominant species) onto the northern Norwegian shelf (Helle and Pennington, 1999). Thus, strong westerly winds are positively related to *C. finmarchicus* abundance on the shelf (Samuelsen et al. 2009). The relationship between *C. finmarchicus* abundance and climate variability in northern Norwegian

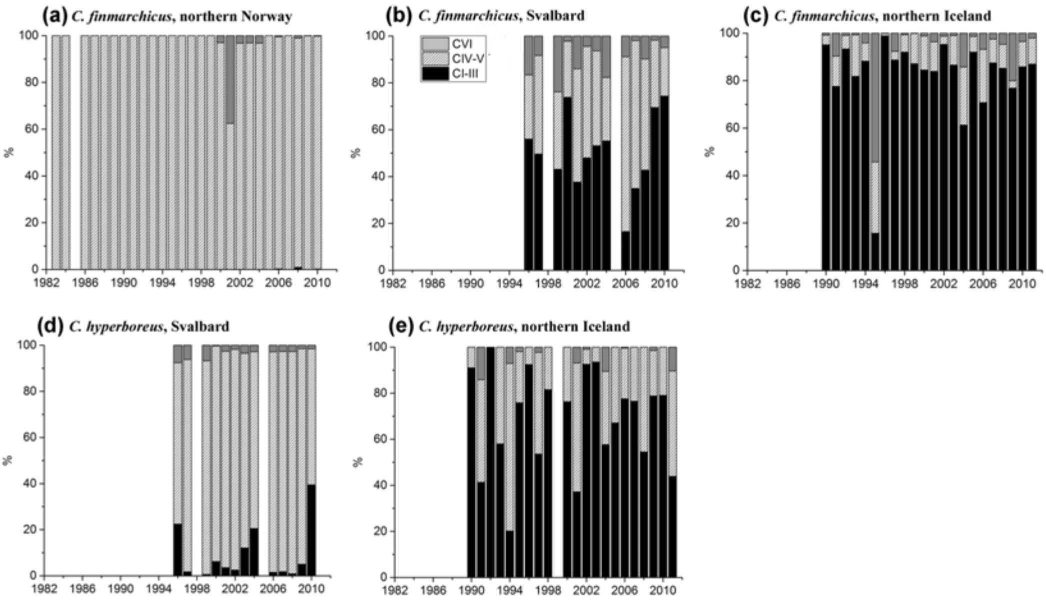


Fig. 5 Stage composition based on averaged abundance (ind m^{-2}) of *Calanus finmarchicus* in northern Norway in October (**a**) and of *C. finmarchicus* and *C. hyperboreus* in Svalbard in July (**b**, **d**) and in northern Iceland in May (**c**, **e**). CI–CIII, CIV–CV, and CVI, denote the combined relative abundance (%) of copepodite stages I through III, IV, and V, and of adult females and males, respectively

Table 3 Temporal change in total abundances (ind m^{-2}) of *Calanus finmarchicus* and *C. hyperboreus* in northern Norway (1983–2010) and northern Iceland (1990–2011) as indicated by Kendall's rank correlation between abundance and year

Species	Location	τ	*P*	*df*
C. finmarchicus	Northern Norway	−0.179	0.003	131
C. hyperboreus		−0.123	0.04	131
C. finmarchicus	Northern Iceland	0.133	0.02	150

No temporal change of abundance was detected in Svalbard

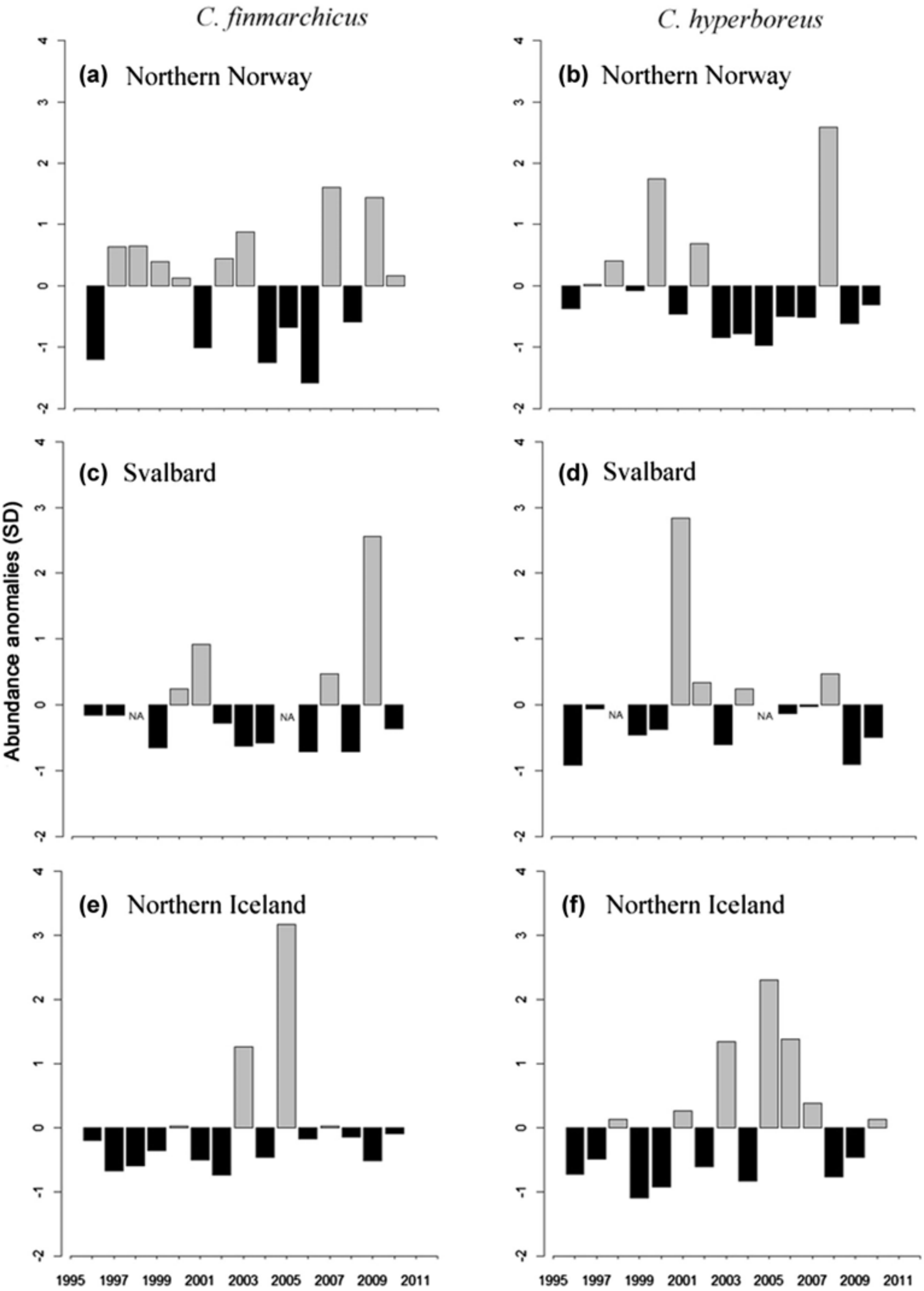
τ Tau Kendall's rank correlation coefficient, *P* significance level of the rank correlation test, *df* degrees of freedom

waters, therefore, may reflect changing fjord productivity and advection levels. Thus, a decreasing trend of both species in northern Norway (Table 3) may be a result of the years with low NAO between 1994 and 2010 (Fig. 3) as was earlier suggested by Skreslet et al. (2015).

Earlier observations in other Norwegian fjords suggest that predation by mesopelagic fish and large copepods can lead to a substantial loss in the abundances of *C. finmarchicus* (Bagøien et al. 2001; Eiane et al. 2002). Thus, although sufficient data on predator abundances in the location in northern Norway are absent, the negative trend in overwintering stocks of *C. finmarchicus* and *C. hyperboreus* may have been caused by predation pressure by fish. In addition, an underlying effect of predation during overwintering months may alter the relationship between abundances and local environmental factors, contributing to the lack of direct relationship between *Calanus* abundances in northern Norway and hydrography or start date of the spring bloom.

The positive relationships between salinity and temperature and the abundance of *Calanus* in Svalbard waters likely reflect variability in the inflow of Atlantic waters originating from the relatively warm and saline WSC (Fig. 1). Such episodes of Atlantic inflow to the western Svalbard shelf are associated with advection of *C. finmarchicus* (Daase and Eiane 2007; Karnovsky et al. 2010) as well as some *C. hyperboreus* (Smith et al. 1985; Hirche 1991). WSC inflow intensifies in summer (Cottier et al. 2005) when our samples were taken, which may have strengthened the *Calanus*–hydrography signal in our data.

An underlying covariation between climate indices and *Calanus* abundance on the western Svalbard shelf may have been masked by time lags (Kwasniewski et al. 2012), caused by the time required for the intensified Atlantic inflow during positive NAO phases to propagate to Arctic latitudes and affect Svalbard shelf waters (Saloranta and Haugan 2001; Visbeck et al. 2013). These climate–zooplankton time lags may exceed several years in Svalbard waters (Kwasniewski et al. 2012). As our data series are


C. finmarchicus
C. hyperboreus
(a) Northern Norway
(b) Northern Norway
(c) Svalbard
(d) Svalbard
(e) Northern Iceland
(f) Northern Iceland
Abundance anomalies (SD)
4
3
2
1
0
-1
-2
NA
NA
NA
NA
1995
1997
1999
2001
2003
2005
2007
2009
2011

◀**Fig. 6** Normalized abundance anomalies (in units of standard deviation, SD) of *Calanus finmarchicus* (*left panels*) and *C. hyperboreus* (*right panels*) during 1996–2010 in northern Norway in October (**a**, **b**), Svalbard in July (**c**, **d**), and northern Iceland in May (**e**, **f**)

too short (15 years) to allow for effective testing of time-lagged effects (Legendre and Legendre 1998), we cannot rule out lagged climate responses in Svalbard *Calanus* populations.

By resolving stage structure, we found that the younger copepodite stages of *C. hyperboreus* responded inversely to AO variability in Svalbard (Fig. 7). Probably, such responses are more apparent in the young stages because of the noise inherent in total abundance estimates at a time when several generations of the long-lived *C. hyperboreus* overlap (Conover 1988). Such noise may weaken signals of interannual climate variability in data sets taken during the productive season.

High AO is associated with warmer winters in the Arctic (Kerr 1999). Increased temperature in surface waters accelerates the development of *C. hyperboreus* nauplii (McLaren and Corkett 1981) and increases food requirement sufficiently to reduce nauplii survival (Jung-Madsen et al. 2013). For the nauplii reaching surface waters in winter, this may result in a temporal mismatch with the food and, subsequently, in low numbers of young copepodites in the following summer (Plourde et al. 2003).

Similar to the situation in Svalbard, we assume that the positive correlation between *C. finmarchicus* and temperature and salinity off northern Iceland (Table 5) was related to the inflow of relatively warm and saline Atlantic water masses of the NIIC (Fig. 1). The NIIC is associated with the advection of *C. finmarchicus* to northern Icelandic waters (Gislason et al. 2009, 2014). In addition, the Atlantic influence increases primary productivity in this area (Astthorsson et al. 1983; Thórdardóttir 1984), hence further strengthening *Calanus* populations through improved feeding conditions. The NIIC inflow has intensified since the mid 1990s (Valdimarsson and Malmberg 2003; Valdimarsson et al. 2012), and we hypothesize that this may have contributed to the increase in *C. finmarchicus* abundance detected in northern Iceland (Table 3). The collinearity between temperature and salinity, both in waters north of northern Iceland and in western Svalbard, strengthens the view that part of the *Calanus* abundance variation may reflect shifting distribution of water masses with a corresponding change in the abundances of the associated fauna (Astthorsson et al. 1983; Daase et al. 2007).

The positive relationship between temperature and the young copepodite stages (CI–CIII) of *C. finmarchicus* in northern Iceland (Fig. 7) also reflects an increase in the abundance of *C. finmarchicus* when warmer Atlantic water masses are dominating in the area (Gislason et al. 2009). Higher abundances of *C. hyperboreus* in northern Iceland tend to occur in years with relatively low Atlantic influence and a high inflow of colder waters of the EIC (Astthorsson et al. 1983) (Fig. 1), which likely explains the inverse relationship with temperature seen in the young copepodite (CI and CII) stages of this species.

We did not detect relationships between climate variability and *C. finmarchicus* in northern Iceland. This result corroborates earlier observations showing that climate variability as measured by NAO correlates neither with hydrography (Ólafsson 1999) nor with zooplankton (Gislason et al. 2009) in northern Iceland. The lack of correlation likely occurs because NIIC inflow in this area is mainly driven by variations in the local north and southerly wind patterns, which appear to vary independently from NAO (Ólafsson 1999). Thus, it may be that the relationship between climate and *C. finmarchicus* in this area are concealed in the data by more pronounced effects of variable NIIC inflow. In contrast, the indicated relationship between climate and *C. hyperboreus* (Table 5) may be linked to the intensified deep-water convection in the Greenland Sea during periods of low NAO (Dickson 1997; Hurrell and Deser 2009). Deep-water transport may enhance the advection of overwintering and ascending *C. hyperboreus* from the main distribution area in the Greenland Sea into the Iceland Sea (Richter 1994; Hirche and Kwasniewski 1997).

Our results indicated that *Calanus* populations in northern Norway responded differently to NAO variability

Table 4 Significant correlations between environmental variables within each location

Variable 1	Variable 2	Years	Kendall's tau	*P*	*df*
Temperature, Svalbard	AO	1996–2010	0.402	<0.001	61
Salinity, Svalbard	NAO	1996–2010	0.307	<0.001	61
Salinity, Svalbard	AO	1996–2010	0.324	<0.001	61
Bloom, Iceland	AO	1990–2011	0.157	0.035	94
Bloom, Svalbard	AO	1996–2010	−0.414	0.002	32

NAO North Atlantic oscillation, *AO* Arctic oscillation, τ Tau Kendall's rank correlation coefficient, *P* significance level of the rank correlation test, *df* degrees of freedom

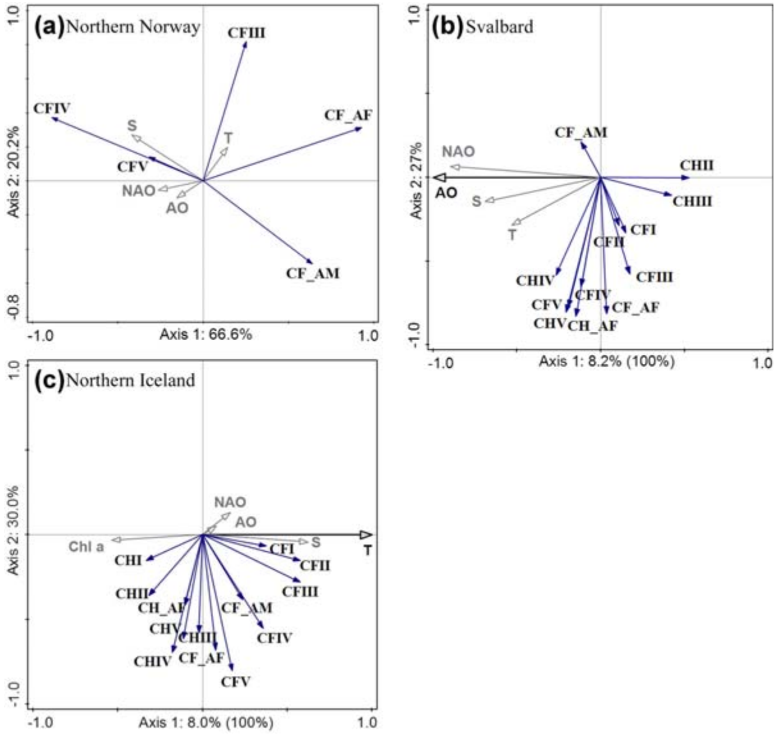


Fig. 7 Ordination plots of environmental data and *Calanus finmarchicus* data from northern Norway (October, 1983–2010; **a**), and environmental data and *C. finmarchicus* and *C. hyperboreus* data from Svalbard (July, 1996–2010; **b**) and northern Iceland (May, 1990–2011; **c**). For northern Norway, environmental variables did not contribute significantly to explaining the variation in the species data, and thus the PCA plot is shown. For Svalbard and northern Iceland, RDA plots are shown. Developmental stages (CI—adults) and environmental variables are represented by *arrows*. Copepodite stage I of *C. hyperboreus* in Svalbard is not shown as this stage was not found. Environmental variables shown as *black arrows* significantly explained the variation in *Calanus* stages' abundances. Environmental variables shown as *grey arrows* had no significant effect on *Calanus* abundances and did not influence RDA. *Arrows* point in the direction of the steepest increase of the respective variable. The angle between *arrows* reflects correlations between the variables. For Svalbard and northern Iceland, percentage values at the axes indicate total variation in data of both species explained by each axis and the amount of the species–environment relationship explained by the axes (*in parenthesis*)

than those in northern Iceland (Table 5). As NAO impacts are mediated through local environmental effects, such as temperature and circulation patterns, the ecological responses tend to differ spatially across the North Atlantic Ocean (Drinkwater et al. 2003). This may explain the lack of similarity in the climate responses of zooplankton in the different parts of the Nordic Seas. For example, high NAO induces winds and precipitation in northern Norway (Hurrell et al. 2001) with possible positive effects on primary production and likely enhances *C. finmarchicus* abundance. In the Labrador Sea, however, high NAO is associated with cooling of surface waters and increased Labrador current flow. This extends the distribution of *C. hyperboreus* onto the Labrador shelf. Concurrently, the Labrador Subarctic Slope Water, rich in *C. finmarchicus*, moves eastwards, decreasing abundance of this species on the Labrador shelf (Greene and Pershing 2000; Johns et al. 2001). Thus, high NAO tends to increase abundances of *C. finmarchicus* in the North East Atlantic (northern Norway) and of *C. hyperboreus* in the North West Atlantic (Labrador shelf). Similarly, high NAO is associated with low *C. finmarchicus* abundance in the North Sea (Fromentin and Planque 1996), but high abundance of the species in the Gulf of Maine (Conversi et al. 2001), which demonstrates variable effects of NAO on *Calanus* in the different locations of the North Atlantic Basin.

Species-specific variability

Calanus hyperboreus abundance was less closely related to environmental variables than the abundance of *C. finmarchicus* (Table 5). We assume that this is because the

Table 5 Significant covariation (Kendall's rank correlation) between environmental indices and total abundances (ind m^{-2}) of *Calanus finmarchicus* and *C. hyperboreus* in northern Norway (1983–2010), Svalbard (1996–2010), and northern Iceland (1990–2011)

Location	Species	Environmental variable	Environmental variable scale	Kendall's tau	*P*	*df*
Northern Norway	*C. finmarchicus*	NAO	Regional	0.386	0.004	26
Northern Norway	*C. finmarchicus*	AO	Regional	0.405	0.003	26
Svalbard	*C. finmarchicus*	Temperature	Local	0.186	0.031	61
Svalbard	*C. finmarchicus*	Salinity	Local	0.271	0.002	61
Svalbard	*C. finmarchicus*	Spring bloom start	Local	0.438	0.001	32
Svalbard	*C. hyperboreus*	Temperature	Local	0.177	0.040	61
Northern Iceland	*C. finmarchicus*	Temperature	Local	0.332	0.000	150
Northern Iceland	*C. finmarchicus*	Salinity	Local	0.234	0.000	150
Northern Iceland	*C. finmarchicus*	Chl *a* concentration	Local	−0.187	0.001	150
Northern Iceland	*C. hyperboreus*	NAO	Regional	−0.131	0.021	150

NAO North Atlantic oscillation, *AO* Arctic oscillation, τ Tau Kendall's rank correlation coefficient, *P* significance level of the rank correlation test, *df* degrees of freedom

Table 6 Hypothesized mechanisms accounting for the observed relationship between *Calanus finmarchicus* and *C. hyperboreus* populations in northern Norway, Svalbard, and northern Iceland, and environmental variability acting on local and regional spatial scales

Location	Spatial scale (environmental variable)	*C. finmarchicus*	*C. hyperboreus*
Northern Norway	Regional (climate)	High abundance at high NAO: increased fjord production and advective influx of individuals from oceanic population	
Svalbard	Local (hydrography)	High abundance when high advective influx from WSC waters	High abundance when high advective influx from WSC waters
	Local (phytoplankton)	High abundance when phytoplankton spring bloom is late: improved feeding conditions for early life stages	
Northern Iceland	Local (hydrography)	High abundance when high advective influx from NIIC	
	Local (phytoplankton)	High abundance at low Chl *a* concentration: high grazing pressure	
	Regional (climate)		High abundance at low NAO: increased deep-water transport of individuals from the Greenland Sea

relatively slow numerical response in the long-lived *C. hyperboreus* (Conover 1988; Hirche 1997) compared to that of *C. finmarchicus* (Østvedt 1955; Tande et al. 1985) weakens abundance responses to changes in the environment (May 1974) and render the link between *C. hyperboreus* dynamics and fluctuations in its local environment less strong than for *C. finmarchicus*. Moreover, *C. hyperboreus* is a capital breeder and, therefore, is capable of producing eggs at depth prior to the spring phytoplankton bloom (Varpe et al. 2009). This strategy likely reduces susceptibility to spring environment in contrast to that of the income breeding *C. finmarchicus*, which usually times egg reproduction to co-occur with the early phase of the spring phytoplankton bloom (Melle and Skjoldal 1998).

Calanus finmarchicus abundance was higher and varied less in all locations than that of *C. hyperboreus* (Table 2; Fig. 4). This difference between the two congeners can be attributed to the geographic location of our study sites, which were in the proximity of the centre of *C. finmarchicus* distribution, i.e. the Norwegian Sea Basin (Broms et al. 2009), or its extensions such as the WSC (Karnovsky et al. 2003). *Calanus hyperboreus*, on the other hand, is an Arctic oceanic species, with a centre of distribution in the Greenland Sea (Richter 1994; Hirche 1997). It is likely, therefore, that our study areas represented fringing or expatriated subpopulations of a much larger *C. hyperboreus* population located in the Greenland Sea proper. Such subpopulations are likely more susceptible to stochastic processes (Hanski 1991), explaining high variability of *C. hyperboreus* in the study locations (Table 2).

Responses to productivity

Calanus finmarchicus abundance was high in years with delayed spring phytoplankton bloom (Table 5). We hypothesize that in such years, the species may have resorted to alternative, likely, microzooplankton food sources (Ohman and Runge 1994; Levinsen et al. 2000; Kwasniewski et al. 2013), which may have allowed for egg production in the absence of high phytoplankton concentrations. *Calanus finmarchicus* nauplii survive long periods of limited food availability (Hygum et al. 2000), and we speculate that years with delayed phytoplankton bloom may coincide with improved feeding conditions for intermediate developmental stages, and thus accelerated *Calanus* growth and development (Campbell et al. 2001; Cook et al. 2007). Such an effect likely enables an earlier descent to the overwintering habitat, thereby limiting exposure to the presumed seasonally increasing predation risk (Fiksen and Carlotti 1998; Pasternak et al. 2001; Varpe et al. 2007) and thus, increasing survival.

We believe that the negative relationship detected between Chl *a* and *C. finmarchicus* in northern Iceland occurred because the abundance of *C. finmarchicus* copepodites increased during the post-bloom phase, when Chl *a* concentration was decreasing (Heath et al. 2000; Head et al. 2013). Thus, rather than reflecting an abundance response to phytoplankton concentrations, this association likely reflected the recruitment of copepodite developmental stages into the population, which typically peaks after the spring Chl *a* maximum (Melle et al. 2014).

Implications for the Basin-scale variability in *Calanus* spp.

Our results suggest that several mechanisms, related to either food availability or advection, may explain the relationship between environmental variability and *Calanus* abundance in the Nordic Seas (Table 6). The environmental drivers involved could be characterized as acting primarily on local (hydrography, food) or regional scale (climate variability), yet the observed relationships largely seem to be brought about by variations in the influence of Atlantic water masses. This is in line with the view that advection-driven connectivity between populations in the subpolar Atlantic is a key to understand *Calanus* ecology (Speirs et al. 2006).

The differences in *Calanus* responses between locations observed in the present study likely reflected variable Atlantic influences on the study areas. In northern Norwegian waters, for instance, the Atlantic influence largely reflects on-shore advection induced by climate-regulated wind stress (Helle and Pennington 1999; Ottersen et al. 2001). In western Svalbard waters, on the other hand, the Atlantic influence seems more controlled by climate-related variability in the WSC (Saloranta and Haugan 2001; Kwasniewski et al. 2012). In waters to the north of Iceland, the coupling between climate variability and Atlantic influence is less clear (Ólafsson 1999; Gislason et al. 2009).

Atlantic inflow to the Nordic Seas (red arrows in Fig. 1) varies with the interaction between the North Atlantic subpolar and subtropical gyres (Hátún et al. 2005), which tends to covary with NAO (Lohmann et al. 2008; Visbeck et al. 2013). Thus, we would expect a relationship between NAO and *Calanus* in all study locations. There are several reasons for why an underlying large-scale covariability may not produce detectable relationships with zooplankton abundances in studies like the present. Firstly, as discussed for Arctic waters above, there may be time lags between climate variability and biological responses (Heath et al. 1999; Blindheim et al. 2000), which makes detection of a climate signal difficult in the relatively short time-series available. Also, the recent warming of the North Atlantic has shifted the distribution of *Calanus* spp. (Chust et al. 2013), and in suboptimal habitats, climate responses may shift or weaken due to alterations in the thermal niche of the populations, as shown in the North Sea (Beaugrand 2012). Thus, it may be difficult to detect climate effects in data sets that include information from fringe populations. Thirdly, the total abundances composed of several cohorts of the multiannual species may not reveal significant covariation between individual developmental stages and climate indices.

Finally, most data sets, on which studies of zooplankton responses to climate are based, contain little information on top-down forcing, or how this may covary with climate. Predation is a significant mechanism regulating *Calanus* populations during both early (Plourde et al. 2009) and older developmental stages (Eiane et al. 2002). Thus, predation on *Calanus* may account for a considerable component of the interannual variability in *Calanus* populations (Ohman and Hirche 2001; Neuheimer et al. 2009). However, predator abundances are also significantly affected by climate variability (Orlova et al. 2010; Valdimarsson et al. 2012; Carscadden et al. 2013) in ways that may alter zooplankton abundances or life history strategies. This knowledge gap may bias our understanding of climate effects on zooplankton. Hence, we suggest that future research on *Calanus* abundance variations should consider both top-down and bottom-up mechanisms in addition to the effects of climate.

Acknowledgements We would like to thank M. Daase and A. Wold (Norwegian Polar Institute) and S. Kwasniewski (Institute of Oceanology, Poland) for their help with data collection and analysis. We are also thankful to H. Petursdottir and S. Sigurgeirsdottir (Marine and Freshwater Research Institute, Iceland), who analysed some of the samples from Northern Iceland, and to T. Thangstad (Institute of Marine Research, Norway) for the help with maps of the sampling locations. The study is done with a contribution from the ARCTOS research network.

Funding The project was funded by the Northern Area Program supported by Conoco Phillips (NSBU-107021) and Lundin Norway (C000353).

References

Aksnes DL, Blindheim J (1996) Circulation patterns in the North Atlantic and possible impact on population dynamics of *Calanus finmarchicus*. Ophelia 44:7–28. doi:10.1080/00785326.1995.10429836

Astthorsson O, Hallgrimsson I, Jónsson GS (1983) Variations in zooplankton densities in Icelandic waters in spring during the years 1961–1982. Rit Fiskideildar 7:73–113

Bagøien E, Kaartvedt S, Aksnes DL, Eiane K (2001) Vertical distribution and mortality of overwintering *Calanus*. Limnol Oceanogr 46:1494–1510. doi:10.4319/lo.2001.46.6.1494

Batchelder HP, Mackas DL, O'Brien TD (2012) Spatial–temporal scales of synchrony in marine zooplankton biomass and abundance patterns: A world-wide comparison. Prog Oceanogr 97:15–30. doi:10.1016/j.pocean.2011.11.010

Beaugrand G (2012) Unanticipated biological changes and global warming. Mar Ecol Prog Ser 445:293–301. doi:10.3354/meps09493

Beaugrand G, Reid PC, Ibañez F, Lindley JA, Edwards M (2002) Reorganization of North Atlantic marine copepod biodiversity and climate. Science 296:1692–1694. doi:10.1126/science.1071329

Blindheim J, Østerhus S (2005) The Nordic Seas, main oceanographic features. In: Drange H, Dokken T, Furevik T, Gerdes R, Berger W (eds) The Nordic Seas: an integrated perspective oceanography, climatology, biogeochemistry, and modeling, vol 158. AGU, Washington, DC, pp 11–37

Blindheim J, Borovkov V, Hansen B, Malmberg SA, Turrell WR, Østerhus S (2000) Upper layer cooling and freshening in the Norwegian Sea in relation to atmospheric forcing. Deep Sea Res Part I 47:655–680. doi:10.1016/S0967-0637(99)00070-9

Broms C, Melle W, Kaartvedt S (2009) Oceanic distribution and life cycle of *Calanus* species in the Norwegian Sea and adjacent waters. Deep Sea Res Part II 56:1910–1921. doi:10.1016/j.dsr2.2008.11.005

Campbell RG, Wagner MM, Teegarden GJ, Boudreau CA, Durbin EG (2001) Growth and development rates of the copepod *Calanus finmarchicus* reared in the laboratory. Mar Ecol Prog Ser 221:161–183. doi:10.3354/meps221161

Carscadden JE, Gjøsæter H, Vilhjálmsson H (2013) Recruitment in the Barents Sea, Icelandic, and eastern Newfoundland/Labrador capelin (*Mallotus villosus*) stocks. Prog Oceanogr 114:84–96. doi:10.1016/j.pocean.2013.05.006

Carstensen J, Weydmann A, Olszewska A, Kwasniewski S (2012) Effects of environmental conditions on the biomass of *Calanus* spp. in the Nordic Seas. J Plankton Res 34:951–966. doi:10.1093/plankt/fbs059

Chust G, Castellani C, Licandro P, Ibaibarriaga L, Sagarminaga Y, Irigoien X (2013) Are *Calanus* spp. shifting poleward in the North Atlantic? A habitat modelling approach. ICES J Mar Sci 71:241–253. doi:10.1093/icesjms/fst147

Cohen J, Barlow M (2005) The NAO, the AO, and global warming: how closely related? J Clim 18:4498–4513. doi:10.1175/JCLI3530.1

Conover RJ (1988) Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the northern hemisphere. Hydrobiologia 167(168):127–142

Conversi A, Piontkovski S, Hameed S (2001) Seasonal and interannual dynamics of *Calanus finmarchicus* in the Gulf of Maine (Northeastern US shelf) with reference to the North Atlantic Oscillation. Deep Sea Res Part II 48:519–530. doi:10.1016/S0967-0645(00)00088-6

Cook KB, Bunker A, Hay S, Hirst AG, Speirs DC (2007) Naupliar development times and survival of the copepods *Calanus helgolandicus* and *Calanus finmarchicus* in relation to food and temperature. J Plankton Res 29:757–767. doi:10.1093/plankt/fbm056

Cottier F, Tverberg V, Inall M, Svendsen H, Nilsen F, Griffiths C (2005) Water mass modification in an Arctic fjord through cross-shelf exchange: the seasonal hydrography of Kongsfjorden, Svalbard. J Geophys Res Oceans 110:C12005. doi:10.1029/2004JC002757

Daase M, Eiane K (2007) Mesozooplankton distribution in northern Svalbard waters in relation to hydrography. Polar Biol 30:969–981. doi:10.1007/s00300-007-0255-5

Daase M, Vik JO, Bagoien E, Stenseth NC, Eiane K (2007) The influence of advection on *Calanus* near Svalbard: statistical relations between salinity, temperature and copepod abundance. J Plankton Res 29:903–911. doi:10.1093/plankt/fbm068

Daase M et al (2013) Timing of reproductive events in the marine copepod *Calanus glacialis*: a pan-Arctic perspective. Can J Fish Aquat Sci 70:871–884. doi:10.1139/cjfas-2012-0401

Dalpadado P, Ellertsen B, Melle W, 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

Dickson B (1997) From the Labrador Sea to global change. Nature 386:649–650. doi:10.1038/386649a0

Dickson R et al (2000) The Arctic ocean response to the North Atlantic oscillation. J Clim 13:2671–2696. doi:10.1175/1520-0442(2000)013<2671:TAORTT>2.0.CO;2

Diel S, Tande K (1992) Does the spawning of *Calanus finmarchicus* in high latitudes follow a reproducible pattern? Mar Biol 113:21–31. doi:10.1007/bf00367634

Drinkwater KF et al (2003) The response of marine ecosystems to climate variability associated with the North Atlantic Oscillation. Geophys Monogr Ser 134:211–234. doi:10.1029/134GM10

Drinkwater K, Colbourne E, Loeng H, Sundby S, Kristiansen T (2013) Comparison of the atmospheric forcing and oceanographic responses between the Labrador Sea and the Norwegian and Barents seas. Prog Oceanogr 114:11–25. doi:10.1016/j.pocean.2013.03.007

Eiane K, Aksnes DL, Ohman MD, Wood S, Martinussen MB (2002) Stage-specific mortality of *Calanus* spp. under different predation regimes. Limnol Oceanogr 47:636–645. doi:10.4319/lo.2002.47.3.0636

Ellertsen B, Fossum P, Sundby S, Tilseth S (1987) The effect of biological and physical factors on the survival of Arcto-Norwegian cod and the influence on recruitment variability. In: Loeng H (ed) The effect of oceanographic conditions on distribution and population dynamics of commercial fish stocks in the Barents Sea: proceedings of the third Soviet-Norwegian Symposium, Murmansk, 26–28 May 1986. Institute of Marine Research, Bergen, pp 101–126

Eloire D, Somerfield PJ, Conway DVP, Halsband-Lenk C, Harris R, Bonnet D (2010) Temporal variability and community composition of zooplankton at station L4 in the Western Channel: 20 years of sampling. J Plankton Res 32:657–679. doi:10.1093/plankt/fbq009

Falk-Petersen S, Sargent JR, Middleton C (1986) Level and composition of triacylglycerols and wax esters in commercial capelin oils from the Barents Sea fishery, 1983. Sarsia 71:49–54. doi:10.1080/00364827.1986.10419673

Falk-Petersen S, Pavlov V, Timofeev S, Sargent J (2007) Climate variability and possible effects on arctic food chains: the role of *Calanus*. In: Ørbæk J, Kallenborn R, Tombre I, Hegseth E, Falk-Petersen S, Hoel A (eds) Arctic alpine ecosystems and people in a changing environment. Springer, Berlin, pp 147–166. doi:10.1007/978-3-540-48514-8_9

Falk-Petersen S, Mayzaud P, Kattner G, Sargent JR (2009) Lipids and life strategy of Arctic *Calanus*. Mar Biol Res 5:18–39. doi:10.1080/17451000802512267

Fiksen Ø, Carlotti F (1998) A model of optimal life history and diel vertical migration in *Calanus finmarchicus*. Sarsia 83:129–147. doi:10.1080/00364827.1998.10413678

Fromentin J, Planque B (1996) *Calanus* and environment in the eastern North Atlantic. 2. Influence of the North Atlantic Oscillation on *C. finmarchicus* and *C. helgolandicus*. Mar Ecol Prog Ser 134:111–118. doi:10.3354/meps134111

Gabrielsen TM et al (2012) Potential misidentifications of two climate indicator species of the marine arctic ecosystem: *Calanus glacialis* and *C. finmarchicus*. Polar Biol 35:1621–1628. doi:10.1007/s00300-012-1202-7

Gislason A, 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

Gislason A, Petursdottir H, Astthorsson OS, Gudmundsson K, Valdimarsson H (2009) Inter-annual variability in abundance and community structure of zooplankton south and north of Iceland in relation to environmental conditions in spring 1990–2007. J Plankton Res 31:541–551. doi:10.1093/plankt/fbp007

Gislason A, Petursdottir H, Gudmundsson K (2014) Long-term changes in abundance of *Calanus finmarchicus* south and north of Iceland in relation to environmental conditions and regional diversity in spring 1990–2013. ICES J Mar Sci 71:2539–2549. doi:10.1093/icesjms/fsu098

Greene CH, Pershing AJ (2000) The response of *Calanus finmarchicus* populations to climate variability in the Northwest Atlantic: basin-scale forcing associated with the North Atlantic Oscillation. ICES J Mar Sci 57:1536–1544. doi:10.1006/jmsc.2000.0966

Greene CH et al (2003) Trans-Atlantic responses of *Calanus finmarchicus* populations to basin-scale forcing associated with the North Atlantic Oscillation. Prog Oceanogr 58:301–312. doi:10.1016/j.pocean.2003.08.009

Halvorsen E (2015) Significance of lipid storage levels for reproductive output in the Arctic copepod *Calanus hyperboreus*. Mar Ecol Prog Ser 540:259–265. doi:10.3354/meps11528

Hansen B, Østerhus S (2000) North Atlantic-Nordic Seas exchanges. Prog Oceanogr 45:109–208. doi:10.1016/S0079-6611(99)00052-X

Hansen MO, Nielsen TG, Stedmon CA, Munk P (2012) Oceanographic regime shift during 1997 in Disko Bay, Western Greenland. Limnol Oceanogr 57:634–644

Hanski I (1991) Single-species metapopulation dynamics: concepts, models and observations. In: Metapopulation dynamics: empirical and theoretical investigations. Academic Press, Cambridge, pp 17–38. doi: 10.1016/B978-0-12-284120-0.50005-X

Hátún H, Sandø AB, Drange H, Hansen B, Valdimarsson H (2005) Influence of the Atlantic Subpolar Gyre on the thermohaline circulation. Science 309:1841–1844

Head EJH, Melle W, Pepin P, Bagøien E, Broms C (2013) On the ecology of *Calanus finmarchicus* in the Subarctic North Atlantic: a comparison of population dynamics and environmental conditions in areas of the Labrador Sea-Labrador/Newfoundland Shelf and Norwegian Sea Atlantic and Coastal Waters. Prog Oceanogr 114:46–63. doi:10.1016/j.pocean.2013.05.004

Heath MR et al (1999) Climate fluctuations and the spring invasion of the North Sea by *Calanus finmarchicus*. Fish Oceanogr 8:163–176. doi:10.1046/j.1365-2419.1999.00008.x

Heath MR et al (2000) 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

Helle K, Pennington M (1999) The relation of the spatial distribution of early juvenile cod (*Gadus morhua* L.) in the Barents Sea to zooplankton density and water flux during the period 1978-1984. ICES J Mar Sci 56:15–27. doi:10.1006/jmsc.1998.0427

Henson SA, Dunne JP, Sarmiento JL (2009) Decadal variability in North Atlantic phytoplankton blooms. J Geophys Res Oceans 114:C04013. doi:10.1029/2008JC005139

Hirche H-J (1991) Distribution of dominant calanoid copepod species in the Greenland sea during late fall. Polar Biol 11:351–362. doi:10.1007/BF00239687

Hirche H-J (1997) Life cycle of the copepod *Calanus hyperboreus* in the Greenland Sea. Mar Biol 128:607–618. doi:10.1007/s002270050127

Hirche H-J, Kwasniewski S (1997) Distribution, reproduction and development of *Calanus* species in the Northeast water in relation to environmental conditions. J Mar Syst 10:299–317. doi:10.1016/S0924-7963(96)00057-7

Hirche H-J, Niehoff B (1996) Reproduction of the Arctic copepod *Calanus hyperboreus* in the Greenland Sea-field and laboratory observations. Polar Biol 16:209–219. doi:10.1007/BF00392894

Hirche HJ, Hagen W, Mumm N, Richter C (1994) The Northeast Water polynya, Greenland Sea. 3. Meso- and macrozooplankton distribution and production of dominant herbivorous copepods during spring. Polar Biol 14:491–503. doi:10.1007/BF00239054

Hurrell JW (1995) Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. Science 269:676–679. doi:10.1126/science.269.5224.676

Hurrell JW, Deser C (2009) North Atlantic climate variability: the role of the North Atlantic Oscillation. J Mar Syst 78:28–41. doi:10.1016/j.jmarsys.2008.11.026

Hurrell JW, Kushnir Y, Visbeck M (2001) The North Atlantic Oscillation. Science 291:603–605. doi:10.1126/science.1058761

Hygum BH, Rey C, Hansen BW (2000) Growth and development rates of *Calanus finmarchicus* nauplii during a diatom spring bloom. Mar Biol 136:1075–1085. doi:10.1007/s002270000313

Johns DG, Edwards M, Batten SD (2001) Arctic boreal plankton species in the Northwest Atlantic. Can J Fish Aquat Sci 58:2121–2124. doi:10.1139/f01-156

Jung-Madsen S, Nielsen TG, Grønkjær P, Hansen BW, Møller EF (2013) Early development of *Calanus hyperboreus* nauplii: response to a changing ocean. Limnol Oceanogr 58:2109–2121. doi:10.4319/lo.2013.58.6.2109

Karnovsky NJ, KwaznieswkI S, Weslawski JM, Walkusz W, Beszczynska-möller A (2003) Foraging behavior of little auks in a heterogeneous environment. Mar Ecol Prog Ser 253:289–303. doi:10.3354/meps253289

Karnovsky N et al (2010) Foraging distributions of little auks *Alle alle* across the Greenland Sea: implications of present and future Arctic climate change. Mar Ecol Prog Ser 415:283–293. doi:10.3354/meps08749

Kendall MG, Gibbons JD (1990) Rank correlation methods. Edward Arnold, London

Kerr RA (1999) A new force in high-latitude climate. Science 284:241–242. doi:10.1126/science.284.5412.241

Kjellerup S, Dünweber M, Swalethorp R, Nielsen T, Møller EF, Markager S, Hansen BW (2012) Effects of a future warmer ocean on the coexisting copepods *Calanus finmarchicu*s and *C. glacialis* in Disko Bay, western Greenland. Mar Ecol Prog Ser 447:87–108. doi:10.3354/meps09551

Koenig WD (2002) Global patterns of environmental synchrony and the Moran effect. Ecography 25:283–288. doi:10.1034/j.1600-0587.2002.250304.x

Kwasniewski S et al (2012) Interannual changes in zooplankton on the West Spitsbergen Shelf in relation to hydrography and their consequences for the diet of planktivorous seabirds. ICES J Mar Sci 69:890–901. doi:10.1093/icesjms/fss076

Kwasniewski S, Walkusz W, Cottier FR, Leu E (2013) Mesozooplankton dynamics in relation to food availability during spring and early summer in a high latitude glaciated fjord (Kongsfjorden), with focus on *Calanus*. J Mar Syst 111–112:83–96. doi:10.1016/j.jmarsys.2012.09.012

Legendre P, Legendre LF (1998) Numerical ecology. Elsevier, Amsterdam

Levinsen H, Jefferson TT, Nielsen TG, Hansen BW (2000) On the trophic coupling between protists and copepods in arctic marine ecosystems. Mar Ecol Prog Ser 204:65–77

Lindeque PK, Hay SJ, Heath MR, Ingvarsdottir A, Rasmussen J, Smerdon GR, Waniek JJ (2006) Integrating conventional microscopy and molecular analysis to analyse the abundance and distribution of four *Calanus* congeners in the North Atlantic. J Plankton Res 28:221–238. doi:10.1093/plankt/fbi115

Loeng H, Drinkwater K (2007) An overview of the ecosystems of the Barents and Norwegian Seas and their response to climate variability. Deep Sea Res Part II 54:2478–2500. doi:10.1016/j.dsr2.2007.08.013

Lohmann K, Drange H, Bentsen M (2008) Response of the North Atlantic subpolar gyre to persistent North Atlantic oscillation like forcing. Clim Dyn 32:273–285. doi:10.1007/s00382-008-0467-6

Mackas DL, Beaugrand G (2010) Comparisons of zooplankton time series. J Mar Syst 79:286–304. doi:10.1016/j.jmarsys.2008.11.030

Maritorena S, Siegel DA (2005) Consistent merging of satellite ocean color data sets using a bio-optical model. Remote Sens Environ 94:429–440. doi:10.1016/j.rse.2004.08.014

Maritorena S, d'Andon OHF, Mangin A, Siegel DA (2010) Merged satellite ocean color data products using a bio-optical model: characteristics, benefits and issues. Remote Sens Environ 114:1791–1804. doi:10.1016/j.rse.2010.04.002

McLaren IA, Corkett CJ (1981) Temperature-dependent growth and production by a marine copepod. Can J Fish Aquat Sci 38:77–83. doi:10.1139/f81-010

Melle W, Skjoldal HR (1998) Reproduction and development of *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* in the Barents Sea. Mar Ecol Prog Ser 169:211–228. doi:10.3354/meps169211

Melle W, Ellertsen B, Skjoldal HR (2004) Zooplankton: the link to higher trophic levels. In: Skjoldal HR (ed) The Norwegian Sea ecosystem. Tapir Academic Press, Trondheim, pp 137–202

Melle W et al (2014) The North Atlantic Ocean as habitat for *Calanus finmarchicus*: environmental factors and life history traits. Prog Oceanogr 129:244–284. doi:10.1016/j.pocean.2014.04.026

Neuheimer AB, Gentleman WC, Galloway CL, Johnson CL (2009) Modeling larval *Calanus finmarchicus* on Georges Bank: time-varying mortality rates and a cannibalism hypothesis. Fish Oceanogr 18:147–160. doi:10.1111/j.1365-2419.2009.00503.x

Niehoff B, Hirche H-J, Båmstedt U (2000) The reproduction of *Calanus finmarchicus* in the Norwegian Sea in spring. Sarsia 85:15–22. doi:10.1080/00364827.2000.10414552

Ohman MD, Hirche HJ (2001) Density-dependent mortality in an oceanic copepod population. Nature 412:638–641. doi:10.1038/35088068

Ohman D, Runge JA (1994) Sustained fecundity when phytoplankton resources are in short supply: omnivory by *Calanus finmarchicus* in the Gulf of St. Lawrence. Limnol Oceanogr 39:21–36. doi:10.4319/lo.1994.39.1.0021

Ólafsson J (1999) Connections between oceanic conditions off N-Iceland, Lake Myvatn temperature, regional wind direction variability and the North Atlantic Oscillation. Rit Fiskideildar/J Mar Res Inst 16:41–58

Orlova E, Rudneva G, Renaud P, Eiane K, Savinov V, Yurko A (2010) Climate impacts on feeding and condition of capelin *Mallotus villosus* in the Barents Sea: evidence and mechanisms from a 30 year data set. Aquat Biol 10:105–118. doi:10.3354/ab00265

Østvedt OJ (1955) Zooplankton investigations from the Weather ship M in the Norwegian Sea, 1948-1949. Hvalradets Skr 40:1–93

Ottersen G, Planque B, Belgrano A, Post E, Reid P, Stenseth N (2001) Ecological effects of the North Atlantic Oscillation. Oecologia 128:1–14. doi:10.1007/s004420100655

Pasternak A, Arashkevich E, Tande K, Falkenhaug T (2001) Seasonal changes in feeding, gonad development and lipid stores in *Calanus finmarchicus* and *C. hyperboreus* from Malangen, northern Norway. Mar Biol 138:1141–1152. doi:10.1007/s002270100553

Perry RI, Batchelder HP, Mackas DL, Chiba S, Durbin E, Greve W, Verheye HM (2004) Identifying global synchronies in marine zooplankton populations: issues and opportunities. ICES J Mar Sci 61:445–456. doi:10.1016/j.icesjms.2004.03.022

Persson J, Stige LC, Stenseth NC, Usov N, Martynova D (2012) Scale-dependent effects of climate on two copepod species, *Calanus glacialis* and *Pseudocalanus minutus*, in an Arctic-boreal sea. Mar Ecol Prog Ser 468:71–83. doi:10.3354/meps09944

Planque B, Taylor AH (1998) Long-term changes in zooplankton and the climate of the North Atlantic. ICES J Mar Sci 55:644–654. doi:10.1006/jmsc.1998.0390

Planque B, Hays GC, Ibanez F, Gamble JC (1997) Large scale spatial variations in the seasonal abundance of *Calanus finmarchicus*. Deep Sea Res Part I 44:315–326. doi:10.1016/S0967-0637(96)00100-8

Plourde S, Joly P, Runge JA, Dodson J, Zakardjian B (2003) Life cycle of *Calanus hyperboreus* in the lower St. Lawrence Estuary and its relationship to local environmental conditions. Mar Ecol Prog Ser 255:219–233. doi:10.3354/meps255219

Plourde S, Maps F, Joly P (2009) Mortality and survival in early stages control recruitment in *Calanus finmarchicus*. J Plankton Res 31:371–388. doi:10.1093/plankt/fbn126

R Core Team (2016) R: a language and environment for statistical computing. R foundation for Statistical Computing, Vienna

Richter C (1994) Regional and seasonal variability in the vertical distribution of mesozooplankton in the Greenland Sea. Berichte zur Polarforschung (Reports on Polar Research) 154

Sætre R, Skjoldal HR, Gjertsen K (2004) The Norwegian Sea ecosystem. Tapir Academic Press, Trondheim

Saloranta TM, Haugan PM (2001) Interannual variability in the hydrography of Atlantic water northwest of Svalbard. J Geophys Res Oceans 106:13931–13943. doi:10.1029/2000JC000478

Samuelsen A, Huse G, Hansen C (2009) Shelf recruitment of *Calanus finmarchicus* off the west coast of Norway: role of physical processes and timing of diapause termination. Mar Ecol Prog Ser 386:163–180. doi:10.3354/meps08060

Siegel DA, Doney SC, Yoder JA (2002) The North Atlantic spring phytoplankton bloom and Sverdrup's Critical depth hypothesis. Science 296:730–733. doi:10.1126/science.1069174

Skreslet S, Borja A (2003) Interannual correlation between hemispheric climate and northern Norwegian wintering stocks of two *Calanus* spp. In: ICES Marine Science Symposia, pp 390–392

Skreslet S, Olsen K, Chelak M, Eiane K (2015) NE Atlantic zooplankton wintering in fjord habitats responds to hemispheric climate. J Plankton Res 37:773–789. doi:10.1093/plankt/fbv032

Smith SL, Smith WO, Codispoti LA, Wilson DL (1985) Biological observations in the marginal ice zone of the East Greenland Sea. J Mar Res 43:693–717. doi:10.1357/002224085788440303

Søreide JE, Leu EVA, Berge J, Graeve M, Falk-Petersen S (2010) Timing of blooms, algal food quality and *Calanus glacialis* reproduction and growth in a changing Arctic. Glob Change Biol 16:3154–3163. doi:10.1111/j.1365-2486.2010.02175.x

Speirs DC, Gurney WS, Heath MR, Horbelt W, Wood SN, De Cuevas BA (2006) Ocean-scale modelling of the distribution, abundance, and seasonal dynamics of the copepod *Calanus finmarchicus*. Mar Ecol Prog Ser 313:173–192. doi:10.3354/meps313173

Steele M, Ermold W, Zhang J (2008) Arctic Ocean surface warming trends over the past 100 years. Geophys Res Lett 35:L02614. doi:10.1029/2007GL031651

Sundby S (2000) Recruitment of Atlantic cod stocks in relation to temperature and advection of copepod populations. Sarsia 85:277–298. doi:10.1080/00364827.2000.10414580

Tande KS, Miller CB (2000) Population dynamics of *Calanus* in the North Atlantic: results from the trans-Atlantic study of *Calanus finmarchicus*. ICES J Mar Sci 57:1527. doi:10.1006/jmsc.2000.0983

Tande KS, Hassel A, Slagstad D (1985) Gonad maturation and possible life cycle strategies in *Calanus finmarchicus* and *Calanus glacialis* in the northwestern part of the Barents Sea. In: Marine Biology of Polar Regions and Effects of Stress on Marine Organisms: Proceedings of the 18th European Marine Biology Symposium, University of Oslo, Norway, 14–20 August 1983. Interscience Wiley, pp 141–155

ter Braak CJF, Smilauer P (2012) CANOCO reference manual and user's guide to canoco for windows: software for ordination (Version 5.0). Centre for Biometry, Wageningen

Thórdardóttir T (1984) Primary production north of Iceland in relation to water masses in May–June 1970–1980. ICES CM 50:20

Turner JT, Borkman DG, Hunt CD (2006) Zooplankton of Massachusetts Bay, USA, 1992-2003: relationships between the copepod *Calanus finmarchicus* and the North Atlantic Oscillation. Mar Ecol Prog Ser 311:115–124. doi:10.3354/meps311115

UNESCO/SCOR (1996) Determination of photosynthetic pigments in seawater. Monographs in oceanographic methodology, vol 1. UNESCO/SCOR, Paris

Unstad KH, Tande KS (1991) Depth distribution of *Calanus finmarchicus* and *C. glacialis* in relation to environmental conditions in the Barents Sea. Polar Res 10:409–420. doi:10.1111/j.1751-8369.1991.tb00662.x

Valdimarsson H, Malmberg S-A (1999) Near-surface circulation in Icelandic waters derived from satellite tracked drifters. Rit Fiskideild 16:23–40

Valdimarsson H, Malmberg S-A (2003) Hydrographic conditions in Icelandic waters, 1990–1999. ICES Mar Sci Symp 219:50–60

Valdimarsson H, Astthorsson OS, Palsson J (2012) Hydrographic variability in Icelandic waters during recent decades and related changes in distribution of some fish species. ICES J Mar Sci 69:816–825. doi:10.1093/icesjms/fss027

Varpe Ø, Fiksen Ø, Slotte A (2005) Meta-ecosystems and biological energy transport from ocean to coast: the ecological importance of herring migration. Oecologia 146:443–451. doi:10.1007/s00442-005-0219-9

Varpe Ø, Jørgensen C, Tarling GA, Fiksen Ø (2007) Early is better: seasonal egg fitness and timing of reproduction in a zooplankton life-history model. Oikos 116:1331–1342. doi:10.1111/j.0030-1299.2007.15893.x

Varpe Ø, Jørgensen C, Tarling GA, Fiksen Ø (2009) The adaptive value of energy storage and capital breeding in seasonal environments. Oikos 118:363–370. doi:10.1111/j.1600-0706.2008.17036.x

Villarino E, Chust G, Licandro P, Butenschon M, Ibaibarriaga L, Larranaga A, Irigoien X (2015) Modelling the future biogeography of North Atlantic zooplankton communities in response to climate change. Mar Ecol Prog Ser 531:121–142. doi:10.3354/meps11299

Visbeck M, Chassignet EP, Curry RG, Delworth TL, Dickson RR, Krahmann G (2013) The Ocean's response to north atlantic oscillation variability. In: The North Atlantic Oscillation: climatic significance and environmental impact. American Geophysical Union, pp 113–145. doi:10.1029/134GM06

Walczowski W, Piechura J, Goszczko I, Wieczorek P (2012) Changes in Atlantic water properties: an important factor in the European Arctic marine climate. ICES J Mar Sci 69:864–869. doi:10.1093/icesjms/fss068

Wassmann P et al (2006) Food webs and carbon flux in the Barents Sea. Prog Oceanogr 71:232–287. doi:10.1016/j.pocean.2006.10.003

Wassmann P, Duarte CM, AgustÍ S, Sejr MK (2011) Footprints of climate change in the Arctic marine ecosystem. Glob Change Biol 17:1235–1249. doi:10.1111/j.1365-2486.2010.02311

Paper III

A comparison of interannual variations in phenology in two North-East Atlantic populations of *Calanus finmarchicus* using vertical life table approach

Marina Espinasse[1], Claudia Halsband[2], Øystein Varpe[2,3], Astthor Gislason[4], Kristinn Gudmundsson[4], Stig Falk-Petersen[2,5], Ketil Eiane[1]

[1] Faculty of Biosciences and Aquaculture, Nord University, P.O Box 1490, N-8049 Bodø, Norway,

[2]Akvaplan-niva, Fram Centre, P.O. Box 6606 Langnes, N-9296 Tromsø, Norway

[3] The University Centre in Svalbard (UNIS), P.O. Box 156, N-9171 Longyearbyen, Norway

[4] Marine and Freshwater Research Institute, Skulagata 4, P.O. Box 1390, 121 Reykjavik, Iceland

[5] Norwegian Polar Institute, Fram Centre, P.O Box 6606 Langnes, N-9296 Tromsø, Norway

Corresponding author: Marina Espinasse
E-mail: ecologM@hotmail.com

Abstract

We studied variability in phenology of the marine copepod *Calanus finmarchicus* in two locations in the North-East Atlantic: Svalbard and northern Iceland, where sampling was done in summer and spring, respectively. We base our study on four indices of phenology developed for stage structured (copepodite stages) data series of limited seasonal coverage. The variation of the four indices was compared within each location and between locations, and their suitability for analysis of seasonally restricted time-series was discussed. The phenology of both populations was related to local environmental factors (hydrography and primary productivity) induced by Atlantic water inflow, while large-scale climate showed less direct effect on *C. finmarchicus* phenology. In both locations, *C. finmarchicus* phenology seemed to advance in warmer conditions. The study results also suggest that vertical phenological indices, i.e. based on interannual changes in stage structure, are useful approaches to investigate zooplankton phenology, especially when data series covering the whole year are unavailable. The two vertical indices, AAD and AWS, are applicable regardless of the timing of sampling, while PDI and CV should be applied for early and late sampling season, respectively. We propose that in studies of zooplankton phenology, where multiple phenological indices are needed, at least the index AAD and either CV or PDI are applied.

Introduction

The timing of life cycle events (phenology) plays a central role in the adaptation of organisms to their environment (Varpe et al., 2007, McNamara and Houston, 2008) and can have significant effects on the fitness of an organism. Phenological traits tend to be flexible and, therefore, may readily change in response to the environmental variability (Post, 2013). Thus, studies of phenology may reveal species-environment relationships and provide new perspectives on species-specific responses to complex environmental fluctuations such as interannual climate variability (Parmesan and Yohe, 2003).

The last decades have seen an accumulation of evidence in support of climate change affecting marine ecosystems in the North Atlantic (Steele et al., 2008, Walczowski et al., 2012) and the Arctic ocean (Wassmann et al., 2011). Such effects of climate change on marine ecosystems may result in large-scale regime shifts (Beaugrand et al., 2015), but more commonly, they are related to subtle changes in hydrography and oceanic circulation that lead to fluctuations in population size and phenological shifts observable on local or regional scales (Greene and Pershing, 2007, Hollowed and Sundby, 2014, Drinkwater et al., 2003).

Many marine planktonic species are particularly sensitive to climate variability because ambient water temperature may directly affect their physiological processes and alter the dynamics of the pelagic environment through effects on thermal stratification and vertical mixing (Hays et al., 2005, Beaugrand, 2005, Edwards, 2009). For herbivorous plankton, fitness depends on their ability to time their reproduction relative to the timing of the phytoplankton spring bloom (Varpe, 2012, Daase et al., 2013). This is because temporal and spatial overlap between the food-sensitive early developmental stages of herbivorous zooplankton and narrow production peaks of their phytoplankton food result in an increased survival probability, according to the match-mismatch hypothesis (Cushing, 1990). However, as climate change may alter timing and succession in plankton communities (Beaugrand et al., 2003, Edwards and Richardson, 2004), the temporal match between phytoplankton and zooplankton may weaken and lead to mis-match (Durant et al., 2007). The consequences of such miss-matching may reduce food web productivity in high-latitude pelagic ecosystems, where the relatively short productive season leaves only a limited time window for the positive growth (Leu et al., 2011).

The primarily herbivorous calanoid copepods *Calanus finmarchicus* is the key trophic link in pelagic ecosystems throughout the North Atlantic, connecting primary production to higher trophic levels (Falk-Petersen et al., 2007). *C. finmarchicus* has its core area of distribution in the Norwegian Sea, and its presence is associated with waters of Atlantic origin throughout most of the North Atlantic area (Jaschnov, 1970, Tande, 1991, Smith et al., 1985). *C. finmarchicus* usually has a one-year life cycle and reproduces in surface waters shortly after the spring phytoplankton bloom, usually, from March to May (Wiborg, 1954, Sømme, 1934, Melle and Skjoldal, 1998).

C. finmarchicus life cycle includes six naupliar (NI to NVI) and six copepodite developmental stages, including early copepodites (CI to CIII), late copepodites (CIV to CV), and adult males and females (CVI). Molting from one developmental stage to the next one is often associated with important life cycle events such as start of feeding (NIII), maturation (CIV), reproduction (CVI) and hibernation (CIII-CV) (Mauchline, 1998).

Due to its ecological importance and sensitivity to climate, *C. finmarchicus* is often a target for studies of phenology of marine zooplankton (Maps et al., 2012, Varpe, 2012). However, precise quantification of the timing of life-history events in zooplankton populations can be challenging, as data series remain scarce. The phenological changes in *Calanus* can be assessed by various phenological proxies based on the total abundance or the abundance of developmental stages. Commonly used indices of phenology include the timing of abundance peak (Chiba et al., 2006, Chiba et al., 2008, Mackas et al., 2012), the passage of the cumulative percentiles of abundance (Greve et al., 2001, Greve et al., 2005), the ratio of CV copepodites to total abundance (Batten et al., 2003, Mackas et al., 1998, Mackas et al., 2007), and the population development index (PDI), i.e., the proportion of early developmental stages in the population (Head et al., 2013). As such indices tend to vary in their sensitivity, applying several indices may allow for capturing different patterns of phenological variability and more responses of phenology to environment (Thackeray et al., 2012, Thackeray et al., 2013).

It is suggested that *C. finmarchicus* stocks dwelling in different oceanographical domains have desynchronized phenological cycles, and therefore, are likely to be affected differently by a rising sea temperature (Kvile et al., 2014, Planque et al., 1997, Daase et al., 2013). One reason for this is that changes in local hydrography may trigger a phenological shift in *Calanus* (Kristiansen et al., 2015), but may also reflect that population at extremes of the distributional range may differ in sensitivity to environmental variability relative to populations near the core distributional area (Beaugrand et al., 2013). Thus, more knowledge is needed to understand how environmental variability is manifested in *C. finmarchicus* phenology.

Here, we study the phenology of *Calanus finmarchicus* in two locations in the North-East Atlantic: in waters off western Svalbard and northern Iceland. We quantify interannual variation in the species phenology by the use of phenological indices based on the population stage structure. We aim to disentangle relationships between *C. finmarchicus* phenology and interannual environmental variability acting on local and regional scales.

Material and methods

Study areas

The present study was based on yearly samples obtained along two transects in the North-East Atlantic: in Kongsfjorden on the western coast of Svalbard and on the shelf off northern Iceland (Fig. 1). Kongsfjorden (maximum depth ~ 400 m) is a glacial fjord, which is influenced by both Atlantic water masses through the West Spitsbergen Current (WSC; Fig.1), and by Arctic water masses from a coastal current (Svendsen et al., 2002, Hop et al., 2006). After year 2000, Kongsfjorden experienced extensive intrusions of Atlantic water masses, which increased heat content and reduced seasonal ice-cover in the fjord in winter (Cottier et al., 2007). The northern Icelandic shelf is affected by Atlantic water masses through the Northern Icelandic Irminger Current (NIIC; Fig.1) as well as by Arctic water masses of the East Greenland Current (EGC) originating in the Arctic Ocean (Fig. 1).

Calanus stage structure

In Kongsfjorden, Svalbard, zooplankton samples were collected by the Norwegian Polar Institute and The University Centre in Svalbard at 4 stations (Kb0 – Kb3; ca 79°N, 12°E; Fig.1) in July yearly from 1996 to 2010, except 1998 and 2005 (Table I). Station Kb0 was not sampled in 1996. Samples were taken with a Multinet (Hydrobios Ltd.; 0.25 m^2 mouth area and 180 μm mesh size) from near the seabed to the surface in standard depth bins (Table I). *Calanus* spp. abundance (ind m^{-2}) was calculated by summing estimates over all depth bins and assuming 100% filtering efficiency of the net.

In northern Iceland, zooplankton was collected at 6 stations (Sigl2 - Sigl7; ca 67°N, 18.5°W; Fig.1) by the Marine and Freshwater Research institute in Iceland in May every year from 1990 to 2011 (Sigl 6 was not sampled in 2007). In 1990 and 1991, a Hensen plankton net (0.42 m^2 mouth area and 200 μm mesh size) was used, while all subsequent sampling was done with a WP2 plankton net (0.25 m^2 aperture and 200 μm mesh size). Plankton nets were towed vertically from 50 m to the surface. Despite sampling in surface waters only, underestimation of *Calanus* counts in northern Iceland was likely minimal because *Calanus* tend to reside in surface waters at the time of sampling (Gislason and Silva, 2012). For samples collected by the Hensen net, abundance estimates (ind m^{-2}) were calculated assuming 100% filtering efficiency of the net, whereas estimates from the WP2 net were based on the water volume measured with a flowmeter (HydroBios Ltd.) mounted on the mouth of the net. We assumed that the two nets had the same characteristics with respect to sampling copepodite stages of *C. finmarchicus*.

All zooplankton samples were preserved in a 4% formaldehyde-in-seawater solution until enumeration in the lab. Species separation of *Calanus* in Svalbard and northern Iceland was based on prosome length distributions (Unstad and Tande, 1991, Hirche et al., 1994) and was done for randomly selected sub-samples. However, in both study locations, there might be some misidentifications of *C. finmarchicus* with the other species of the genus *Calanus*.

Environmental data

Salinity and temperature profiles were obtained by CTD casts (Sea-Bird Electronics) at each sampling station. In northern Iceland, Chl *a* concentrations were also estimated by filtering 1 or 2 L water samples collected at 10 and 30 m depth onto GF/C glass fibre filters, that were subsequently analysed by a spectrophotometer as described in UNESCO/SCOR (1996).

As a proxy for the timing of the phytoplankton spring bloom each year, we estimated the start date of the phytoplankton spring bloom for 1998 -2010 (2011 for northern Iceland). These estimates were based on remote sensing data on Chl *a* concentration collected by NASA (SeaWiFS and Aqua-MODIS) and ESA (MERIS), available from the Hermes portal of the European Service of Ocean Colour (http://hermes.acri.fr/index.php?class=archive). The downloaded Chl *a* levels (8-day intervals from site-specific areas of approximately 4.63 x 4.63 km) were merged by a Garver, Sieleg and Maritorena (GSM) model (Maritorena et al., 2010, Maritorena and Siegel, 2005). In Svalbard, Chl *a* measurements were taken from a rectangular area outside the fjord (from 78°45′N to 79°14′N and from 9°30’ to 11°E) to avoid distortion by terrestrial inference. For northern Iceland, remote Chl *a* measurements were from a rectangular area (from 66°30′ N to 67°45′N and from 17°30′W to 19°15′W), which enclosed all sampled stations. The Chl *a* levels were extracted in R (R Core Team, 2016), using the package *ncdf4* (v.1.9; Pierce 2013). Missing values of the Chl *a* data were interpolated by the *approx* function in R. We estimated the date of the spring bloom start as the first day of the year when Chl *a* concentration exceeded 5% above the median Chl *a* concentration for that year and location (Henson et al., 2009, Siegel et al., 2002).

As a proxy for large-scale environmental variability, we used annual values for the North Atlantic Oscillation index (NAO) and the Arctic Oscillation index (AO) (Hurrell, 1995, Cohen and Barlow, 2005) downloaded from the Climate Data Guide (http://www.climatedataguide.ucar.edu) and from the US National Oceanographic and Atmospheric Administration (NOAA; http://www.cpc.noaa.gov/), respectively.

Phenological indices and data analysis

To test for the temporal trends in the environmental variables, a non-parametric correlation test was applied (Kendall, 1970), because data deviated from normality and contained outliers.

So far, only a few data series from the Sub-Arctic region covered the whole life cycle of *Calanus*. This complicates studies of *Calanus* phenology, as most of the phenological indices rely on seasonal development of the populations. To overcome this problem, we applied a set of alternative phenological indices that rely on stage-structured abundance data (copepodite stages only), collected over a short period of time. Such application of "snapshot data", covering a restricted period of a life-cycle, is referred to as a vertical life table approach (Aksnes and Ohman, 1996, Aksnes et al., 1997). We applied four vertical indices calculated as follows.

First, we computed the proportion of copepodite stage V (CV) to total abundance of copepodite stages (CVT) (Mackas et al., 2007, Mackas et al., 1998),

$$CVT = \frac{N_{CV}}{N_{tot}} \tag{1}$$

where N_{CV} is the abundance of stage CV, and N_{tot} is the total abundance of *Calanus* copepodites in the sample.

Secondly, we used the population development index (PDI), calculated as the proportion of early copepodite stages (CI to CIII) to total abundance of copepodites (Head et al., 2013),

$$PDI = \frac{N_{CI-CIII}}{N_{tot}} \tag{2}$$

where $N_{CI\text{-}CIII}$ is the sum of the abundances of copepodites stages CI to CIII.

Thirdly, we used the average weighted stage (AWS) of the population,

$$\text{AWS} = \sum_{k=1}^{6} (w * k) / \sum_{k=1}^{6} w \tag{3}$$

where w is the proportion (%) of each copepodite stage in the sample and k is the order of copepodite stage.

Finally, we estimated the average age in days (AAD) of the population:

$$AAD = \sum_{i=1}^{6}(D * x) \,/ \sum_{i=1}^{6} x \qquad (4)$$

where *x* is the proportion of each copepodite stage in a sample and *D* is the duration in days of each copepodite stage as function of temperature (McLaren, 1978, Campbell et al., 2001).

$$D = a(T - \alpha)^{-2.05} \qquad (5)$$

where *T* is ambient temperature in 0-50 m, and a and α are empirically fitted constants.

Index CVT is reflecting the variation of the older copepodites in the population, while PDI represents the variation of the early copepodites only. On the other hand, AWS would depend on the variation of both early and older life stages, and AAD is the only index that reflects the age of the population in a given temperature conditions. Therefore, the four phenological indices represent different stages and aspects of *Calanus* life cycle and when analysed together, are expected to provide a more complete overview of the species phenological variation. This is especially relevant for our study, where *C. finmarchicus* from Svalbard and northern Iceland were sampled at different times of year, and copepodite stage compositions were different in the two locations. Thus, indices based on both early (PDI) and late (CVT) copepodites were included in the study.

Phenological indices deviated from normality and contained outliers, hence a non-parametric statistical test was preferred throughout the data analysis. To test for trends in the phenological indices caused by the variability in the time of sampling between years (Table I) we used a non-parametric correlation test (Kendall’s correlation) and found that generally, the phenological indices were subject to such trends. Therefore, the phenological indices were de-trended with a moving average method (Legendre and Legendre, 1998). First, we estimated average phenological indices per day within a sampling window each year. The missing values were interpolated using the *mice* package in R (v. 2.25; Van Buuren and Groothuis-Oudshoorn, 2011). Then, a 3-day moving average was applied to smooth the daily average values. The residuals were calculated by subtracting the moving average values from the average values of the phenological indices per day of a year. These residuals, representing a seasonal component of the data-series variability (Turner et al., 2006), were then extracted from the original phenological indices data to yield de-trended data series with respect to the effect of variation in sampling days between years.

To test for collinearity between de-trended phenological indices and to determine relationships between de-trended phenological indices and local environmental variability (temperature, salinity, Chl *a* and the start date of the spring bloom) as well as regional (NAO, AO) environmental variability, Kendall's correlation test was applied. As the index AAD is a function of temperature, it was not correlated against temperature.

Results

Environmental variability

In Svalbard, salinity increased ($\tau = 0.30$, $p = 0.002$), and in northern Iceland, both average temperature and salinity increased over the study period ($\tau = 0.15$, $p = 0.014$ and $\tau = 0.13$, $p = 0.030$, respectively; Fig. 2).

Average (0 - 50 m) temperature in Svalbard and northern Iceland was similar 3.80 °C (range = 1.90 to 5.30) and 3.58°C (range = 0.54 to 5.80), respectively (Fig. 2). Salinity (0 - 50 m) was on average somewhat lower in Svalbard (33.62 psu, range = 30 to 34.4) than in northern Iceland (34.75 psu, range = 34.3 to 35) (Fig. 2).

The average date of the spring bloom start in Svalbard was day 150 (range =130 to 168), and in northern Iceland, it started on average around day 154 (range = 127 to 173) (Fig.3). Average concentration of in situ Chl *a* in northern Iceland was 4.76 mg L^{-1}, (range = 0.31 to 12.0 mg L^{-1}) (Fig.3).

Temperature in Svalbard correlated positively with AO variability ($\tau = 0.40$, $p < 0.001$), while salinity correlated positively with both NAO and AO ($\tau = 0.31$, $p < 0.001$ and $\tau = 0.32$, $p < 0.001$), and the start date of the spring bloom correlated negatively with AO ($\tau = -0.41$, $p = 0.002$). In northern Iceland, only bloom timing correlated with AO ($\tau = 0.16$, $p =0.035$)

During the studied period (1990 - 2011) NAO anomaly was highest in 1990 (3.88) and 2011 (2.95), while the lowest NAO occurred in 2010 (-5.96) (Fig.2). AO variability was synchronous with that of NAO, and highest AO were also observed in 1990 (1.02) and 2011 (0.52), while the lowest AO was in 2010 (-1.04).

C. finmarchicus abundance and stage structure

C. finmarchicus population in Svalbard in July was dominated by early copepodites (CI – CIII) in most years, except 2001, 2006, and 2007, when CIVs and CV were more abundant. In 2003 and 2004, all copepodite abundances were relatively low in Svalbard (Fig. 4).

Early copepodite stages also dominated in the *C. finmarchicus* population in northern Iceland in May. The abundance of early copepodites was highest in 2003 and 2005, while in the preceding years 2002 and 2004, the abundance of early copepodites was relatively low. Older copepodite stages CIV to adults occurred in low numbers and showed little variability throughout the time series in northern Iceland (Fig.4).

Phenological indices

In Svalbard in July the proportion of copepodites CV (CVT) ranged from 0.06 in 2009 to 0.48 in 2006 (Fig. 5). The index CVT was generally low between years 1996 and 2001 (around 0.12). CVT in in northern Iceland in May was very low over the whole time-series (range <0.01 to 0.09).

The population development index (PDI) was generally lower in Svalbard in July (range 0.02 to 0.13) than in northern Iceland in May (range 0.27 to 0.93) (Fig.5). Interannual variability in PDI in Svalbard mirrored that of CVT. In Svalbard, PDI peaked in 2009 (0.68), when the CVT was very low, and the lowest PDI (0.23) coincided with maximal CVT in 2006. In northern Iceland, PDI was high in 1996, 1998, and 2002 (~ 0.93), but was very low in 1995 (0.26). The average weighted stage (AWS) in Svalbard ranged from 3.07 in 2009 and 3.06 in 2008 to 4.18 in 2006. AWS was generally lower in northern Iceland than in Svalbard and ranged from 1.70 in 1998 to 4.15 in 1995. The average age in days (AAD) in Svalbard varied from 38.17 in 2003 to 61.14 in 1999. In northern Iceland, AAD was lowest (27.37) in 2000 and peaked in 1995 (100.38) (Fig.5).

CVT and PDI, as well as CVT and AWS correlated in Svalbard, but AAD did not correlate with the other phenological indices in Svalbard (Table II). In northern Iceland, all phenological indices correlated (Table II).

Phenology and environmental variability

In Svalbard, highest CVT coincided with years with relatively high water temperature and positive AO anomalies (Fig. 2, Fig. 5), thus, CVT correlated positively with both temperature and AO variability. In contrast, PDI in Svalbard correlated negatively with both AO and temperature (Table III). AWS correlated positively with AO and temperature, while AAD correlated negatively with AO and salinity.

In northern Iceland, highest PDI values in 1998 and 2002 coincided with a relatively early spring bloom start (Fig. 3, Fig. 5), and PDI correlated negatively with the spring bloom start, while CVT correlated positively with the spring bloom start. AWS correlated positively with the start date of the spring bloom and Chl *a* concertation. AAD maximum coincided with the coldest year in northern Iceland (1995) and was also high in relatively cold years 2002 and 2007, when salinity was also relatively low (Fig. 2, Fig. 5). Thus, AAD correlated negatively with salinity (Table III).

Discussion

C. finmarchicus phenology and environmental variability

Our results suggest that *Calanus* phenology was related to local environmental variability in both locations. Especially, temperature and the timing of the phytoplankton spring bloom were relevant for explaining year-to-year differences in *Calanus* phenology. Although interannual temperature variations were related to phenology in the same way in the Svalbard and northern Iceland populations, the mechanisms involved were likely different, and partly reflected the difference in the timing of sampling of the two populations.

The relationship between *Calanus* phenology and ambient temperature in Svalbard (Table III) implies that the population consisted of older copepodite stages in years when water temperature was relatively high (2002, 2006). Years with high water temperature likely reflected large influxes of warm Atlantic waters to Konsgfjorden. Such influxes became more frequent after 2000 and resulted in warmer conditions in Kongsfjorden (Walczowski et al., 2012). Increased water temperature probably contributed to faster development of *C. finmarchicus* (Campbell et al., 2001), and thus, a larger fraction of the population had reached older copepodite stages at the time of sampling (July) in relatively warm years assuming that egg laying occurred at relatively similar time each year. In addition, the influx of Atlantic water masses to the western Svalbard shelf is associated with advection of *C. finmarchicus* from the Norwegian Sea (Daase et al., 2007). *C. finmarchicus* cohorts advected from the south spawn earlier than the local population (Kwasniewski et al., 2003), and this may have further contributed to high proportions of older copepodites of *C. finmarchicus* in years with high Atlantic inflow.

In northern Iceland, the interaction between the inflows of Atlantic and Arctic water masses is a key driver of the variability of *C. finmarchicus* ecology (Gislason, 2005). Advection of warmer Atlantic waters from the south-west transports some *C. finmarchicus* to northern Icelandic waters, but also promotes primary productivity, which induces spawning of *C. finmarchicus* (Astthorsson et al., 1983). This results in an increased number of early copepodites of *C. finmarchicus* during sampling in spring. In contrast, years when Arctic water masses dominate in the ecosystem are characterized by reduced planktonic productivity (Thórdardóttir, 1984). Although the spring phytoplankton bloom may start earlier in such years, it often ends already in early May (Gudmundsson, 1998). Shorter blooms may contribute to reduce egg production rate of *C. finmarchicus* (Møller et al., 2016). Thus, we interpret such situations as indicative of unfavorable conditions that may result in reduced spawning of *C. finmarchicus* and lower recruitment of early life stages to the population and possibly, a delayed development from nauplii to early copepodites. This may explain relatively high abundances of overwintering stages and low total C. *finmarchicus* abundance observed in the cold year 1995 in northern Iceland.

AAD was inversely associated with salinity in northern Iceland (Table III), further indicating that in colder years, when the inflow of less saline, Arctic waters was increased (Gudmundsson, 1998), reproduction and recruitment of *C. finmarchicus* was reduced, and thus, the population largely consisted of the overwintering generation.

Climate (as indexed by NAO and AO) did not seem to be a uniform driver of *C. finmarchicus* phenology in the populations studied here, although climate drives the phenology of many marine and terrestrial organisms (Parmesan and Yohe, 2003, Körner and Basler, 2010, Asch, 2015). However, climate effects on *Calanus* populations can be lagged or masked by overlaying effects of local hydrographic variability (Espinasse et al., 2017). In northern Iceland, *Calanu*s variability is largely driven by Atlantic water inflow (Jónsson and Valdimarsson, 2005). This inflow depends largely on the local wind regime, which is typically little affected by NAO or AO variability (Stefánsson and Gudmundsson, 1969). This may have weakened the direct correlation between *C. finmarchicus* phenology and climatic indices in northern Iceland in our data set.

We suggest that the positive effect of AO on *C. finmarchicus* phenology in Svalbard can be explained by local climate and hydrography changes driven by AO variability. In the Arctic, high AO is associated with elevated temperatures (Kerr et al. 1999). This may provide better conditions for *Calanus* growth and development, but this effect is probably complicated and difficult to discern, due to the additional effect of Atlantic water inflow.

Temperature or its correlates – salinity and the timing of primary production in spring, were significant drivers of *C. finmarchicus* phenology in both locations. This supports the notion that temperature plays a primary role for inducing phenological variation in a range of marine and terrestrial animals (Hays et al., 2005, Sparks et al., 2000, Menzel et al., 2006). Temperature effects on plankton are often considered as a part of global warming studies (Edwards and Richardson 2004), and it is suggested that plankton tend to follow an “earlier when warmer” strategy (Mackas et al., 2012). This agrees with the findings of our study. In Svalbard, this strategy likely implied faster development and earlier recruitment to copepodite stages in years with higher water temperature, while in northern Iceland, this was likely mediated by an earlier spawning of *C. finmarchicus* in warm years than in cold years.

Comparison of the phenological indices

The CVT index is used in several studies to time the seasonal peak abundance of copepods (Mackas et al., 2007, Mackas et al., 1998). In our study, we analysed data collected over a relatively short period each year, and identification of seasonal peak would be constrained by sampling time. Thus, we consider CVT more as a proxy for population development progression, because the proportion of older copepodites in *C. finmarchicus* tends to be low during recruitment and is usually higher when the main reproduction season is over (Conover, 1988).

As the data series from Svalbard and northern Iceland were collected at different times of a year, they represent populations that were at different stages of seasonal development. In Svalbard, where data were collected in July, CVT was relatively high and showed considerable variability between years (Fig. 5). Data from northern Iceland were collected in May and contained low proportions of CVs throughout the study period. We attribute this difference to the seasonal progression from early to late copepodites in both locations. In data collected close to the peak of *C. finmarchicus* spawning, as in northern Iceland, CVT was small and showed limited variability between years. Thus, phenological shifts occurring during this season would likely not be detected by the CVT index. A month or more after the peak of spawning in *C. finmarchicus*, when recruits may have already reached stage CV, CVT may be a more efficient identifier of phenological changes.

The PDI index, on the other hand, reflects the dominance of early copepodites and thus, correlated negatively with CVT (Table II). High relative abundance of early copepodites can be observed about a month after the main spawning event in *C. finmarhicus* (Campbell et al., 2001; own observations). PDI, thus, can be a more suitable phenology index in the northern Iceland data set, where sampling was done in spring, the season of the main spawning of *C. finmarchicus*, and the bulk of the population in this location consisted of early copepodite stages.

The variability of AWS seemed to be less dependent on the season of sampling than CVT and PDI, as it showed comparable variability in both locations. Also, AWS strongly correlated with both CVT and PDI in all locations (Table II), suggesting that this index can be useful in cases when the application of either PDI or CVT is problematic.

At higher ambient temperature, the development time of *C. finamrchicus* is shortened (Corkett et al., 1986, McLaren and Corkett, 1981). For example, in 1999 and 2004, water surface temperatures in Svalbard were low. This concurred with a peak in AAD, which implies that in cold years, the development from nauplii to older copepodite stages took relatively longer time. Hence, the AAD index reflects both stage structure and temperature and should be used together with copepodite stage-specific indices CVT and PDI (Table IV).

AAD variability was different from that in the other indices (Fig. 5). During the coldest year in Iceland in our study (1995), both the lowest PDI and highest AWS and AAD occurred. However, during years with near-average temperature, the variability in AAD was not always synchronous with the variability in the other indices (Fig 5). This discrepancy in the synchronization between phenological indices probably occurs, because copepodite stage composition and duration of copepodite stages are non-linearly related to small scale changes in temperature. However, this issue needs more investigation, as currently, the function describing responses of age of the population to temperature, is based on the assumption of constant ambient temperature during copepodite stages development (Corkett et al., 1986), and does not account for temperature changes due to advection of water masses.

Concluding remarks

Similar to the year-to year variability in population abundances (Espinasse et al., 2017), phenological variation in *C. finmarchicus* seemed to reflect environmental variability, most notably, water temperature or salinity (Table IV). Large-scale climate, as indicated by NAO and AO indices, was important for *Calanus* phenology in the Svalbard population only. This effect was likely related to the variability in hydrography and local climate, but these changes were not as clear in northern Icelandic waters.

Our results show that the application of multiple phenological proxies enhanced the identification of environmental factors causing interannual variability in the seasonal development of *C. finmarchicus* despite both data-series were limited to one sampling period each year. We propose that at least two indices should be applied in phenological studies of *Calanus* populations, where the first index (CVT or PDI) is chosen according to the sampling period, and the second is AAD (Table IV).

The role of predation on *Calanus* phenology could not be assessed in this work. This is unfortunate, as predation plays an important role for *Calanus* seasonality (Varpe et al., 2007, Atkinson et al., 2015). Moreover, if temperature also affects abundances and seasonal timing of predators (Durant et al., 2007), this may lead to the development of mismatch, or lack of temporal overlap, between the seasonal peak of zooplankton and planktivorous stages of fish and may eventually change seasonal predation pressure on *Calanus*. However, the responses of *Calanus* phenology to the variation in predation pressure are not fully resolved (Varpe, 2012). Thus, further studies on *Calanus* phenology should also include data on phenology of the main predators, because this would likely provide a more comprehensive picture of *Calanus* seasonal variability (Bandara et al., 2016).

Acknowledgements

We are thankful to M. Daase and A. Wold (Norwegian Polar Institute), S. Sigurgeirsdottir, H. Petursdottir (Marine and Freshwater Research Institute, Iceland) and S. Kwasniewski (Institute of Oceanology, Poland) for their help with data collection and analysis. The study was done with a support from the ARCTOS Research network.

References

Aksnes, D.L., Miller, C.B., Ohman, M.D. & Wood, S.N. (1997). Estimation techniques used in studies of copepod population dynamics - A review of underlying assumptions. *Sarsia,* 82**:** 279-296.

Aksnes, D.L. & Ohman, M.D. (1996). A vertical life table approach to zooplankton mortality estimation. *Limnol Oceanogr,* 41**:** 1461-1469.

Asch, R.G. (2015). Climate change and decadal shifts in the phenology of larval fishes in the California Current ecosystem. *Proceedings of the National Academy of Sciences of the United States of America,* 112**:** E4065-E4074. DOI 10.1073/pnas.1421946112

Astthorsson, O., Hallgrimsson, I. & Jónsson, G.S. (1983). Variations in zooplankton densities in Icelandic waters in spring during the years 1961–1982. *Rit Fiskideildar,* 7**:** 73-113.

Atkinson, A., Harmer, R.A., Widdicombe, C.E., Mcevoy, A.J., Smyth, T.J., Cummings, D.G., Somerfield, P.J., Maud, J.L. & Mcconville, K. (2015). Questioning the role of phenology shifts and trophic mismatching in a planktonic food web. *Prog Oceanogr,* 137, Part B**:** 498-512. DOI 10.1016/j.pocean.2015.04.023

Bandara, K., Varpe, Ø., Søreide, J.E., Wallenschus, J., Berge, J. & Eiane, K. (2016). Seasonal vertical strategies in a high-Arctic coastal zooplankton community. *Mar Ecol Prog Ser,* 555**:** 49-64. DOI: 10.3354/meps11831

Batten, S.D., Welch, D.W. & Jonas, T. (2003). Latitudinal differences in the duration of development of Neocalanus plumchrus copepodites. *Fish Oceanogr,* 12**:** 201-208. DOI 10.1046/j.1365-2419.2003.00233.x

Beaugrand, G. (2005). Monitoring pelagic ecosystems using plankton indicators. *ICES J Mar Sci,* 62**:** 333-338. DOI 10.1016/j.icesjms.2005.01.002

Beaugrand, G., Brander, K.M., Lindley, J.A., Souissi, S. & Reid, P.C. (2003). Plankton effect on cod recruitment in the North Sea. *Nature,* 426**:** 661-664.

Beaugrand, G., Conversi, A., Chiba, S., Edwards, M., Fonda-Umani, S., Greene, C., Mantua, N., Otto, S.A., Reid, P.C., Stachura, M.M., Stemmann, L. & Sugisaki, H. (2015). Synchronous marine pelagic regime shifts in the Northern Hemisphere. *Phil Trans R Soc B,* 370. DOI 10.1098/rstb.2013.0272

Beaugrand, G., Mackas, D. & Goberville, E. (2013). Applying the concept of the ecological niche and a macroecological approach to understand how climate influences zooplankton: Advantages, assumptions, limitations and requirements. *Prog Oceanogr,* 111**:** 75-90. DOI 10.1016/j.pocean.2012.11.002

Campbell, R.G., Wagner, M.M., Teegarden, G.J., Boudreau, C.A. & Durbin, E.G. (2001). Growth and development rates of the copepod Calanus finmarchicus reared in the laboratory. *Mar Ecol Prog Ser,* 221**:** 161-183. DOI 10.3354/meps221161

Chiba, S., Aita, M.N., Tadokoro, K., Saino, T., Sugisaki, H. & Nakata, K. (2008). From climate regime shifts to lower-trophic level phenology: Synthesis of recent progress in retrospective studies of the western North Pacific. *Prog Oceanogr,* 77**:** 112-126. DOI 10.1016/j.pocean.2008.03.004

Chiba, S., Tadokoro, K., Sugisaki, H. & Saino, T. (2006). Effects of decadal climate change on zooplankton over the last 50 years in the western subarctic North Pacific. *Global Change Biol,* 12**:** 907-920. DOI 10.1111/j.1365-2486.2006.01136.x

Cohen, J. & Barlow, M. (2005). The NAO, the AO, and Global Warming: How Closely Related? *J Clim,* 18**:** 4498-4513. DOI 10.1175/JCLI3530.1

Conover, R.J. (1988). Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the northern hemisphere. *Hydrobiologia,* 167/168**:** 127-142.

Corkett, C., Mclaren, I. & Sevigny, J. (1986). The rearing of the marine calanoid copepods *Calanus* finmarchicus (Gunnerus), *C. glacialis* Jaschnov and *C. hyperboreus* Kroyer with comment on the equiproportional rule. IN Schriever, G., Schminke, H. & Shih, C.E. (Eds.) *Syllogeus 58, Proceedings of the second international conference on Copepoda 13–17, August.* Ottawa: The National Museum of Ottawa.

Cottier, F.R., Nilsen, F., Inall, M.E., Gerland, S., Tverberg, V. & Svendsen, H. (2007). Wintertime warming of an Arctic shelf in response to large-scale atmospheric circulation. *Geophys Res Lett,* 34**:** 1-5. DOI 10.1029/2007GL029948

Cushing, D.H. (1990). Plankton Production and Year-class Strength in Fish Populations: an Update of the Match/Mismatch Hypothesis. IN Blaxter, J.H.S. & Southward, A.J. (Eds.) *Adv Mar Biol.* Academic Press.

Daase, M., Falk-Petersen, S., Varpe, O., Darnis, G., Soreide, J.E., Wold, A., Leu, E., Berge, J., Philippe, B. & Fortier, L. (2013). Timing of reproductive events in the marine copepod *Calanus glacialis*: a pan-Arctic perspective. *Can J Fish Aquat Sci,* 70**:** 871-884. DOI 10.1139/cjfas-2012-0401

Daase, M., Vik, J.O., Bagoien, E., Stenseth, N.C. & Eiane, K. (2007). The influence of advection on Calanus near Svalbard: statistical relations between salinity, temperature and copepod abundance. *J Plankton Res,* 29**:** 903-911. DOI 10.1093/plankt/fbm068

Drinkwater, K.F., Belgrano, A., Borja, A., Conversi, A., Edwards, M., Greene, C.H., Ottersen, G., Pershing, A.J. & Walker, H. (2003). the response of marine ecosystems to climate variability associated with the North Atlantic Oscillation. *The North Atlantic Oscillation: Climatic Significance and Environmental Impact.* Washington, DC: American Geophysical Union.

Durant, J.L.M., Hjermann, D.Ã., Ottersen, G. & Stenseth, N.C. (2007). Climate and the match or mismatch between predator requirements and resource availability. *Clim Res,* 33**:** 271-283. DOI 10.3354/cr033271

Edwards, M. (2009). Chapter 12 - Sea Life (Pelagic and Planktonic Ecosystems) as an Indicator of Climate and Global Change. IN Letcher, T.M. (Ed.) *Climate Change.* Amsterdam: Elsevier.

Edwards, M. & Richardson, A.J. (2004). Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature,* 430**:** 881-884.

Espinasse, M., Halsband, C., Varpe, Ø., Gislason, A., Gudmundsson, K., Falk-Petersen, S. & Eiane, K. (2017). The role of local and regional environmental factors for *Calanus finmarchicus* and *C. hyperboreus* abundances in the Nordic Seas. *Polar Biol*. DOI 10.1007/s00300-017-2150-z

Falk-Petersen, S., Pavlov, V., Timofeev, S. & Sargent, J. (2007). Climate variability and possible effects on arctic food chains: The role of Calanus. IN Ørbæk, J., Kallenborn, R., Tombre, I., Hegseth, E., Falk-Petersen, S. & Hoel, A. (Eds.) *Arctic Alpine Ecosystems and People in a Changing Environment.* Springer Berlin Heidelberg.

Gislason, A. (2005). Seasonal and spatial variability in egg production and biomass of *Calanus finmarchicus* around Iceland. *Mar Ecol Prog Ser,* 286**:** 177-192. DOI 10.3354/meps286177

Gislason, A. & 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

Greene, C.H. & Pershing, A.J. (2007). Climate Drives Sea Change. *Science,* 315**:** 1084-1085. DOI 10.1126/science.1136495

Greve, W., Lange, U., Reiners, F. & Nast, J. (2001). Predicting the seasonality of North Sea zooplankton. *Senckenb Marit,* 31**:** 263-268. DOI 10.1007/bf03043035

Greve, W., Prinage, S., Zidowitz, H., Nast, J. & Reiners, F. (2005). On the phenology of North Sea ichthyoplankton. *ICES J Mar Sci,* 62**:** 1216-1223. DOI 10.1016/j.icesjms.2005.03.011

Gudmundsson, K. (1998). Long-term variation in phytoplankton productivity during spring in Icelandic waters. *ICES J Mar Sci,* 55**:** 635-643. DOI 10.1006/jmsc.1998.0391

Hays, G.C., Richardson, A.J. & Robinson, C. (2005). Climate change and marine plankton. *Trends Ecol Evol,* 20**:** 337-344. DOI http://dx.doi.org/10.1016/j.tree.2005.03.004

Head, E.J.H., Melle, W., Pepin, P., Bagøien, E. & Broms, C. (2013). On the ecology of *Calanus finmarchicus* in the Subarctic North Atlantic: A comparison of population dynamics and environmental conditions in areas of the Labrador Sea-Labrador/Newfoundland Shelf and Norwegian Sea Atlantic and Coastal Waters. *Prog Oceanogr,* 114**:** 46-63. DOI 10.1016/j.pocean.2013.05.004

Henson, S.A., Dunne, J.P. & Sarmiento, J.L. (2009). Decadal variability in North Atlantic phytoplankton blooms. *J Geophys Res Oceans,* 114**:** 1-11. DOI 10.1029/2008JC005139

Hirche, H.J., Hagen, W., Mumm, N. & Richter, C. (1994). The Northeast Water polynya, Greenland Sea. III. Meso- and macrozooplankton distribution and production of dominant herbivorous copepods during spring. *Polar Biol,* 14**:** 491-503. DOI 10.1007/BF00239054

Hollowed, A.B. & Sundby, S. (2014). Change is coming to the northern oceans. *Science,* 344**:** 1084-1085.

Hop, H., Falk-Petersen, S., Svendsen, H., Kwasniewski, S., Pavlov, V., Pavlova, O. & Soreide, J.E. (2006). Physical and biological characteristics of the pelagic system across Fram Strait to Kongsfjorden. *Prog Oceanogr,* 71**:** 182-231. DOI 10.1016/j.pocean.2006.09.007

Hurrell, J.W. (1995). Decadal trends in the North Atlantic Oscillation: Regional temperatures and precipitation. *Science,* 269**:** 676-679.

Jaschnov, W.A. (1970). Distribution of Calanus Species in the Seas of the Northern Hemisphere. *Internationale Revue der gesamten Hydrobiologie und Hydrographie,* 55**:** 197-212. DOI 10.1002/iroh.19700550203

Jónsson, S. & Valdimarsson, H. (2005). The flow of Atlantic water to the North Icelandic Shelf and its relation to the drift of cod larvae. *ICES J Mar Sci,* 62**:** 1350-1359. DOI 10.1016/j.icesjms.2005.05.003

Kendall, M.G. (1970). *Rank correlation methods,* London: Griffin.

Körner, C. & Basler, D. (2010). Phenology Under Global Warming. *Science,* 327**:** 1461-1462. DOI 10.1126/science.1186473

Kristiansen, I., Gaard, E., Hátún, H., Jónasdóttir, S. & Ferreira, A.S.A. (2015). Persistent shift of Calanus spp. in the southwestern Norwegian Sea since 2003, linked to ocean climate. *ICES J Mar Sci*. DOI 10.1093/icesjms/fsv222

Kvile, K.O., Dalpadado, P., Orlova, E., Stenseth, N.C. & Stige, L.C. (2014). Temperature effects on Calanus finmarchicus vary in space, time and between developmental stages. *Mar Ecol Prog Ser,* 517**:** 85-104. DOI 10.3354/meps11024

Kwasniewski, S., Hop, H., Falk-Petersen, S. & Pedersen, G. (2003). Distribution of *Calanus* species in Kongsfjorden, a glacial fjord in Svalbard. *J Plankton Res,* 25**:** 1-20. DOI 10.1093/pankt/25.1.1

Legendre, P. & Legendre, L.F. (1998). *Numerical ecology*: Elsevier.

Leu, E., Søreide, J.E., Hessen, D.O., Falk-Petersen, S. & Berge, J. (2011). Consequences of changing sea-ice cover for primary and secondary producers in the European Arctic shelf seas: Timing, quantity, and quality. *Prog Oceanogr,* 90**:** 18-32. DOI 10.1016/j.pocean.2011.02.004

Mackas, D.L., Batten, S. & Trudel, M. (2007). Effects on zooplankton of a warmer ocean: Recent evidence from the Northeast Pacific. *Prog Oceanogr,* 75**:** 223-252. DOI 10.1016/j.pocean.2007.08.010

Mackas, D.L., Goldblatt, R. & Lewis, A.G. (1998). Interdecadal variation in developmental timing of *Neocalanus plumchrus* populations at Ocean Station P in the subarctic North Pacific. *Can J Fish Aquat Sci,* 55**:** 1878-1893. DOI 10.1139/f98-080

Mackas, D.L., Greve, W., Edwards, M., Chiba, S., Tadokoro, K., Eloire, D., Mazzocchi, M.G., Batten, S., Richardson, A.J., Johnson, C., Head, E., Conversi, A. & Peluso, T. (2012). Changing zooplankton seasonality in a changing ocean: Comparing time series of zooplankton phenology. *Prog Oceanogr,* 97-100**:** 31-62. DOI 10.1016/j.pocean.2011.11.005

Maps, F., Runge, J.A., Leising, A., Pershing, A.J., Record, N.R., Plourde, S. & Pierson, J.J. (2012). Modelling the timing and duration of dormancy in populations of *Calanus finmarchicus* from the Northwest Atlantic shelf. *J Plankton Res,* 34**:** 36-54. DOI 10.1093/plankt/fbr088

Maritorena, S., D'andon, O.H.F., Mangin, A. & Siegel, D.A. (2010). Merged satellite ocean color data products using a bio-optical model: Characteristics, benefits and issues. *Remote Sens Environ,* 114**:** 1791-1804. DOI 10.1016/j.rse.2010.04.002

Maritorena, S. & Siegel, D.A. (2005). Consistent merging of satellite ocean color data sets using a bio-optical model. *Remote Sens Environ,* 94**:** 429-440. DOI 10.1016/j.rse.2004.08.014

Mauchline, J. (1998). *The biology of calanoid copepods,* Academic Press.

Mclaren, I.A. (1978). Generation Lengths of Some Temperate Marine Copepods: Estimation, Prediction, and Implications. *Journal of the Fisheries Research Board of Canada,* 35**:** 1330-1342. DOI 10.1139/f78-208

Mclaren, I.A. & Corkett, C.J. (1981). Temperature-Dependent Growth and Production by a Marine Copepod. *Can J Fish Aquat Sci,* 38**:** 77-83. DOI 10.1139/f81-010

Mcnamara, J.M. & Houston, A.I. (2008). Optimal Annual Routines: Behaviour in the Context of Physiology and Ecology. *Philosophical Transactions: Biological Sciences,* 363**:** 301-319. DOI 10.2307/20208431

Melle, W. & Skjoldal, H.R. (1998). Reproduction and development of *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* in the Barents Sea. *Mar Ecol Prog Ser,* 169**:** 211-228. DOI 10.3354/meps169211

Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská, O.G., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Dahl, Å., Defila, C., Donnelly, A., Filella, Y., Jatczak, K., Måge, F., Mestre, A., Nordli, Ø., Peñuelas, J., Pirinen, P., Remišová, V., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A.J.H., Wielgolaski, F.-E., Zach, S. & Zust, A.N.A. (2006). European phenological response to climate change matches the warming pattern. *Global Change Biol,* 12**:** 1969-1976. DOI 10.1111/j.1365-2486.2006.01193.x

Møller, E.F., Bohr, M., Kjellerup, S., Maar, M., Møhl, M., Swalethorp, R. & Nielsen, T.G. (2016). *Calanus finmarchicus* egg production at its northern border. *J Plankton Res*. DOI 10.1093/plankt/fbw048

Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature,* 421**:** 37-42

Planque, B., Hays, G.C., Ibanez, F. & Gamble, J.C. (1997). Large scale spatial variations in the seasonal abundance of Calanus finmarchicus. *Deep Sea Res Part I,* 44**:** 315-326. DOI 10.1016/S0967-0637(96)00100-8

Post, E. (2013). Life History Variation and Phenology. *Ecology of Climate Change: the Importance of Biotic Interactions*. Oxford: Princeton University Press.

R Core Team (2016). R: A language and environment for statistical computing. Vienna, Austria: R foundation for Statistical Computing.

Siegel, D.A., Doney, S.C. & Yoder, J.A. (2002). The North Atlantic Spring Phytoplankton Bloom and Sverdrup's Critical Depth Hypothesis. *Science,* 296**:** 730-733. DOI 10.1126/science.1069174

Smith, S.L., Smith, W.O., Codispoti, L.A. & Wilson, D.L. (1985). Biological observations in the marginal ice zone of the East Greenland Sea. *J Mar Res,* 43**:** 693-717.

Sømme, J.D. (1934). Animal Plankton of the Norwegian Coast Warers and the Open Sea. I. Production of *Calanus finmarchicus* (Gunner) and *Calanus hyperboreus* (Krøyer) in the Lofoten Area. *Report on Norwegian Fishery and Marine Investigations,* 4**:** 1-163.

Sparks, T.H., Jeffree, E.P. & Jeffree, C.E. (2000). An examination of the relationship between flowering times and temperature at the national scale using long-term phenological records from the UK. *International Journal of Biometeorology,* 44**:** 82-87. DOI 10.1007/s004840000049

Steele, M., Ermold, W. & Zhang, J. (2008). Arctic Ocean surface warming trends over the past 100 years. *Geophys Res Lett,* 35**:** L02614. DOI 10.1029/2007GL031651

Stefánsson, U. & Gudmundsson, G. (1969). Hydrographic conditions off the northeast coast of Iceland in relation to meteorological factors. *Tellus,* 21**:** 245-258.

Svendsen, H., Beszczynska-Møller, A., Hagen, J.O., Lefauconnier, B., Tverberg, V., Gerland, S., Ørbøk, J.B., Bischof, K., Papucci, C., Zajaczkowski, M., Azzolini, R., Bruland, O., Wiencke, C., Winther, J.-G. & Dallmann, W. (2002). The physical environment of Kongsfjorden–Krossfjorden, an Arctic fjord system in Svalbard. *Polar Res,* 21**:** 133-166. DOI 10.1111/j.1751-8369.2002.tb00072.x

Tande, K.S. (1991). *Calanus* in North Norwegian fjords and in the Barents Sea. *Polar Res,* 10**:** 389-408. DOI 10.1111/j.1751-8369.1991.tb00661.x

Thackeray, S.J., Henrys, P.A., Feuchtmayr, H., Jones, I.D., Maberly, S.C. & Winfield, I.J. (2013). Food web de-synchronization in England's largest lake: an assessment based on multiple phenological metrics. *Glob Chang Biol,* 19**:** 3568-80. DOI 10.1111/gcb.12326

Thackeray, S.J., Henrys, P.A., Jones, I.D. & Feuchtmayr, H. (2012). Eight decades of phenological change for a freshwater cladoceran: what are the consequences of our definition of seasonal timing? *Freshwat Biol,* 57**:** 345-359. DOI 10.1111/j.1365-2427.2011.02614.x

Thórdardóttir, T. (1984). *Primary production north of Iceland in relation to water masses in May-June 1970-1980*.

Turner, J.T., Borkman, D.G. & Hunt, C.D. (2006). Zooplankton of Massachusetts Bay, USA, 1992-2003: relationships between the copepod Calanus finmarchicus and the North Atlantic Oscillation. *Mar Ecol Prog Ser,* 311**:** 115-124. DOI 10.3354/meps311115

Unesco/Scor (1996). *Determination of photosynthetic pigments in seawater. Monograpths in Oceanographic Methodology.1.,* Paris: UNESCO/SCOR.

Unstad, K.H. & Tande, K.S. (1991). Depth distribution of *Calanus finmarchicus* and *C. glacialis* in relation to environmental conditions in the Barents Sea. *Polar Res,* 10**:** 409-420. DOI 10.1111/j.1751-8369.1991.tb00662.x

Van Buuren, S. & Groothuis-Oudshoorn, K. (2011). MICE: Multivariate Imputation by Chained Equations in R. *Journal of Statistical Software,* 45**:** 1-67.

Varpe, O. (2012). Fitness and phenology: annual routines and zooplankton adaptations to seasonal cycles. *J Plankton Res,* 34**:** 267-276. DOI 10.1093/plankt/fbr108

Varpe, Ø., Jørgensen, C., Tarling, G.A. & Fiksen, Ø. (2007). Early is better: seasonal egg fitness and timing of reproduction in a zooplankton life-history model. *Oikos,* 116**:** 1331-1342. DOI 10.1111/j.0030-1299.2007.15893.x

Walczowski, W., Piechura, J., Goszczko, I. & Wieczorek, P. (2012). Changes in Atlantic water properties: an important factor in the European Arctic marine climate. *ICES J Mar Sci,* 69**:** 864-869. DOI 10.1093/icesjms/fss068

Wassmann, P., Duarte, C.M., Agustí, S. & Sejr, M.K. (2011). Footprints of climate change in the Arctic marine ecosystem. *Global Change Biol,* 17**:** 1235-1249. DOI 10.1111/j.1365-2486.2010.02311.x

Wiborg, K.F. (1954). *Investigations on zooplankton in coastal and offshore waters of western and northwestern Norway with special reference to the copepods*, Bergen: Director of Fisheries, G. Griegs boktr.

Tables

Table I. Sampling information and total number of samples from Svalbard and northern Iceland

Location and stations	Sampling gears	Sampling depth, m	Year, season and range of sampling days	Total number of samples
Svalbard			July 1996-2010, Days 182-215	
KB0	Multinet	315-200-100-50-20-0		50
KB1		352-200-100-50-20-0		
KB2		330-200-100-50-20-0		
KB3		329-200-100-50-20-0		
Northern Iceland, Sigl 2-7	Hensen net, WP2 net	50	May 1990-2011, Days 137-153	131

Table II. Significant correlations (Kendall's rank correlation, $p \leq 0.05$) between de-trended phenological indices of *C. finmarchicus* from Svalbard and northern Iceland. The negative and positive values stand for negative and positive correlation, respectively. NS = not significant correlation. Indices are abbreviated as follows: CVT, the proportion of copepodites CV to total abundance; PDI, population development index; AWS, average weighted stage; AAD, average age in days.

Location	Phenological indices		
Svalbard	CVT	PDI	AWS
CVT			
PDI	-0.63		
AWS	0.59	-0.73	
AAD	NS	NS	NS
Northern Iceland			
CVT			
PDI	-0.54		
AWS	0.49	-0.75	
AAD	0.17	-0.39	0.39

Table III. Statistically significant correlations between phenological indices of *C. finmarchicus* from Svalbard and northern Iceland and environmental parameters NAO, (North Atlantic Oscillation), AO (Arctic Oscillation), T (temperature), S (salinity), Bloom (start date of the spring bloom), Chl *a* (in situ chlorophyll *a* concentration); τ, Kendall's rank correlation coefficient; *P*, significance level of the rank correlation test; *df*, degrees of freedom. Indices are abbreviated as follows: CVT, the proportion of copepodites CV to total abundance; PDI, population development index; AWS, average weighted stage; AAD, average age in days.

location and species	Phenological index	Environmental variables	*df*	τ	*P*
Svalbard,	CVT	AO	48	0.31	0.002
C. finmarchicus		T	48	0.42	<0.001
	PDI	AO	48	-0.37	<0.001
		T	48	-0.34	<0.001
	AWS	AO	48	0.23	0.024
		T	48	0.24	0.016
	AAD	AO	48	-0.37	<0.001
		S	48	-0.30	0.002
Northern Iceland,	CVT	Bloom	81	0.22	0.005
C. finmarchicus	PDI	Bloom	81	-0.19	0.015
	AWS	Chl *a*	129	0.13	0.022
		Bloom	81	0.26	0.001
	AAD	S	129	-0.32	<0.001

Table IV. Suitable phenological indices and suggested environmental drivers of *C. finmarchicus* phenology in Svalbard and northern Iceland. Indices are abbreviated as follows: CVT, the proportion of copepodites CV to total abundance; PDI, population development index; AWS, average weighted stage; AAD, average age in days.

Location and season	Suitable vertical indices	Main drivers of phenology	Mechanisms of relationships
Svalbard, July	CVT, AAD	Local: temperature	The inflow of warm Atlantic water masses accelerates the development of *C. finmarchicus*
		Regional: AO	Warmer temperatures during high AO – faster development of copepodites
Northern Iceland, May	PDI, AAD	Local: hydrography and its effects on bloom dynamics Regional: none	The inflow of Arctic waters decreases reproduction and development of early life stages. The inflow of warmer Atlantic waters has the opposite effect on *C. finmarchicus* phenology

Figure legends

Figure 1. Location of the sampling of *C. finmarchicus* data in Svalbard in July and in northern Iceland in May. The sampling site in Svalbard is a transect of four stations (depth range 315 - 352), in northern Iceland – a transect of six stations (depth range 230 – 700 m). Red and black arrows denote Atlantic and Polar water currents, respectively.

Figure 2. Average temperature (0 – 50 m, °C), NAO and AO annual indices (**a**) and salinity (**b**) over the sampling stations in Svalbard and northern Iceland.

Figure 3. The average start day of the spring phytoplankton bloom in Svalbard and northern Iceland (**a**) and in situ Chl *a* concetration in northern Iceland (**b**). The spring bloom start was estimated from the remote sensors data on Chl *a* concetration. For the details of the calculation of the start day of the bloom, see text.

Figure 4. Average copepodite abundances from the transect in Svalbard in July (left), and the transect in northern Iceland in May (right). CI, CII, CIII, CIV, CV denote copepodite stage abundances I through V, and CVI is the sum of adult male and female abundances.

Figure 5. Yearly averages of de-trended phenological indices in Svalbard in July (left) and northern Iceland in May (right). Indices are abbreviated as follows: CVT, the proportion of copepodites CV to total abundance; PDI, population development index; AWS, average weighted stage; AAD, average age in days.

Fig.1

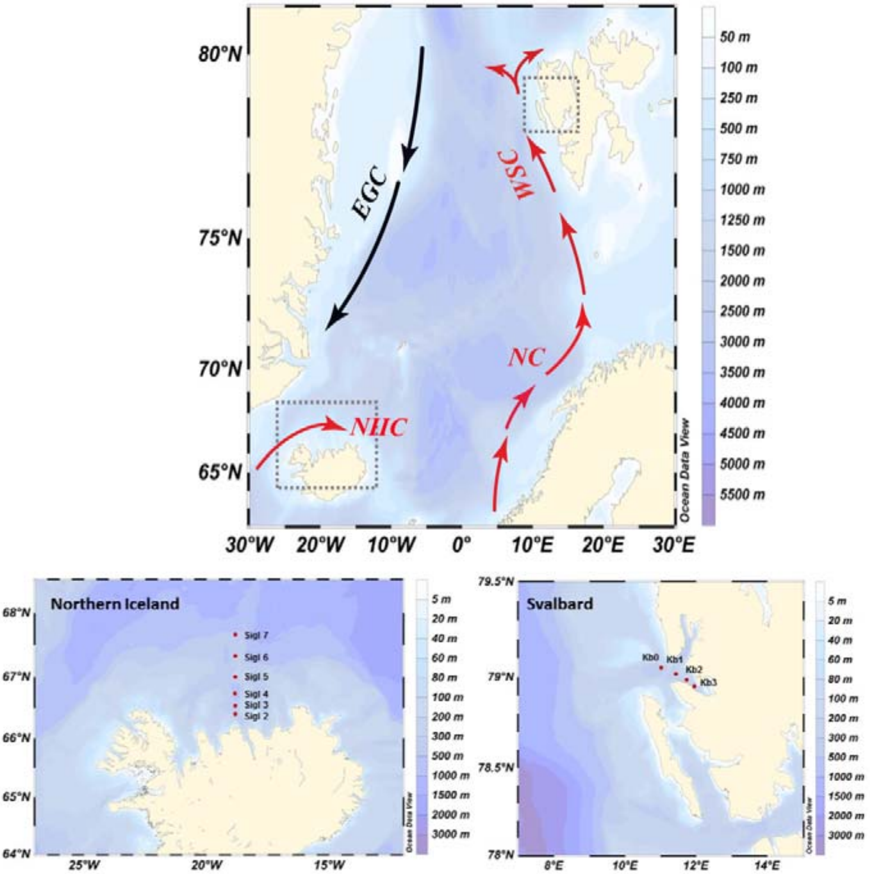

80°N
75°N
70°N
65°N
EGC
WSC
NC
NHC
50 m
100 m
250 m
500 m
750 m
1000 m
1250 m
1500 m
2000 m
2500 m
3000 m
3500 m
4000 m
4500 m
5000 m
5500 m
Ocean Data View
30°W
20°W
10°W
0°
10°E
20°E
30°E
Northern Iceland
68°N
67°N
66°N
65°N
64°N
Sigl 7
Sigl 6
Sigl 5
Sigl 4
Sigl 3
Sigl 2
5 m
20 m
40 m
60 m
80 m
100 m
200 m
300 m
500 m
1000 m
1500 m
2000 m
3000 m
Ocean Data View
25°W
20°W
15°W
Svalbard
79.5°N
79°N
78.5°N
78°N
Kb0
Kb1
Kb2
Kb3
5 m
20 m
40 m
60 m
80 m
100 m
200 m
300 m
500 m
1000 m
1500 m
2000 m
3000 m
Ocean Data View
8°E
10°E
12°E
14°E

Fig. 2

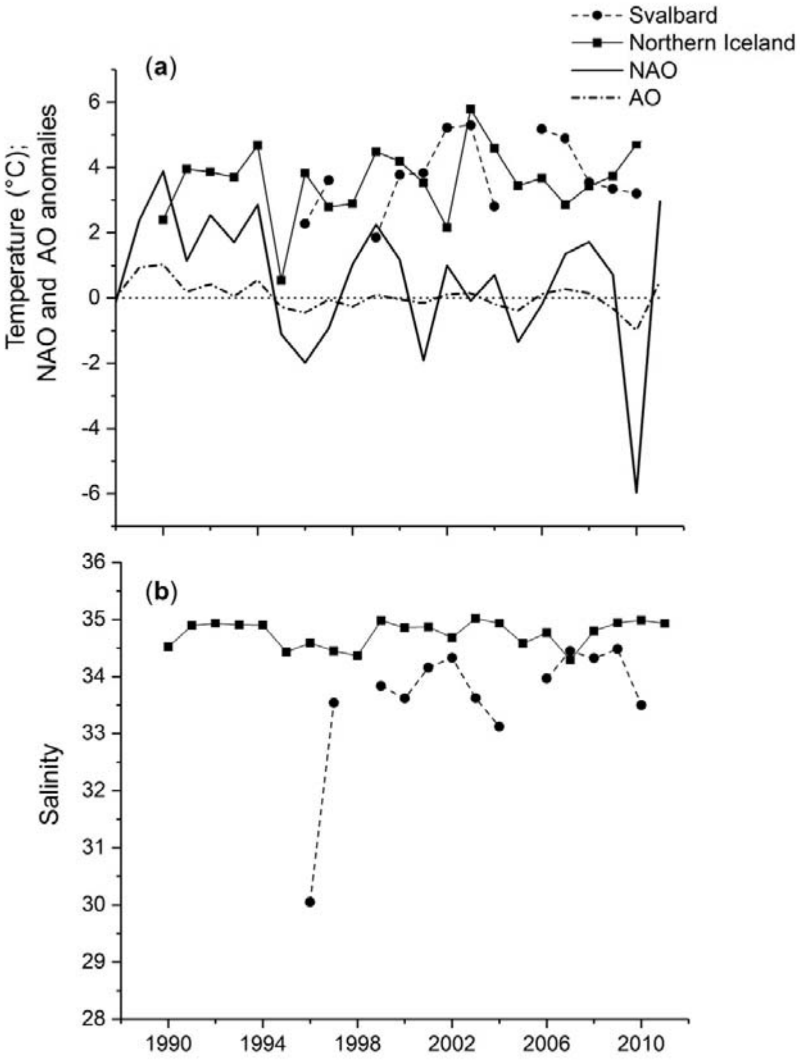

Svalbard
Northern Iceland
NAO
AO
(a)
Temperature (°C);
NAO and AO anomalies
6
4
2
0
-2
-4
-6
(b)
Salinity
36
35
34
33
32
31
30
29
28
1990
1994
1998
2002
2006
2010

Fig.3

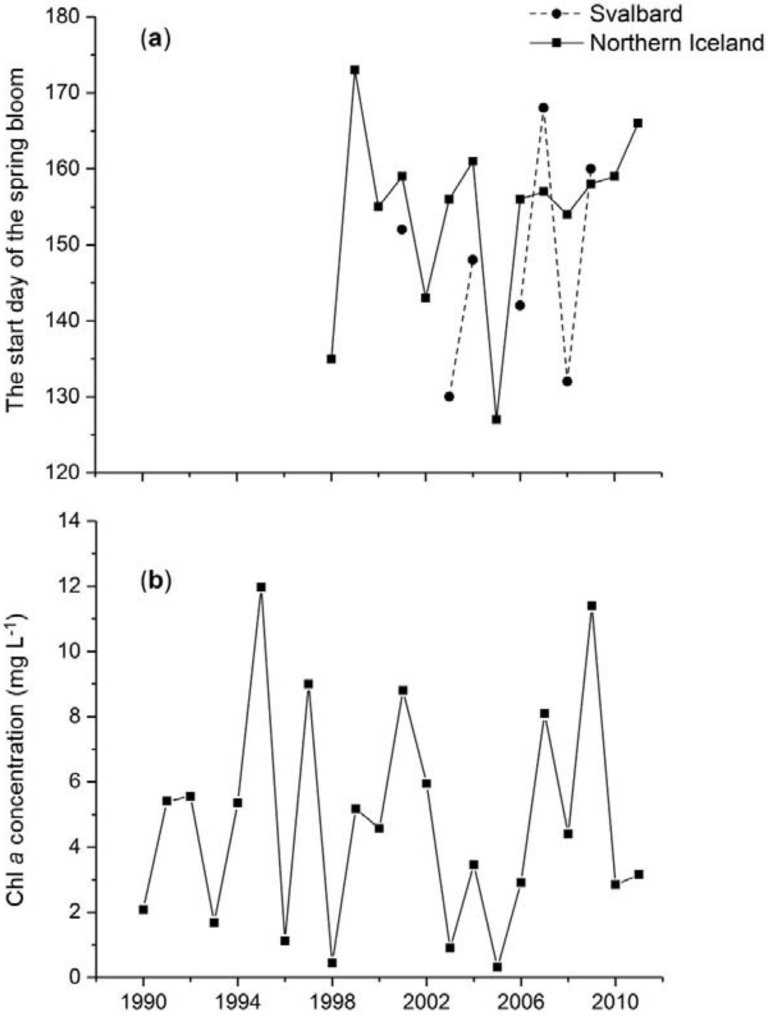
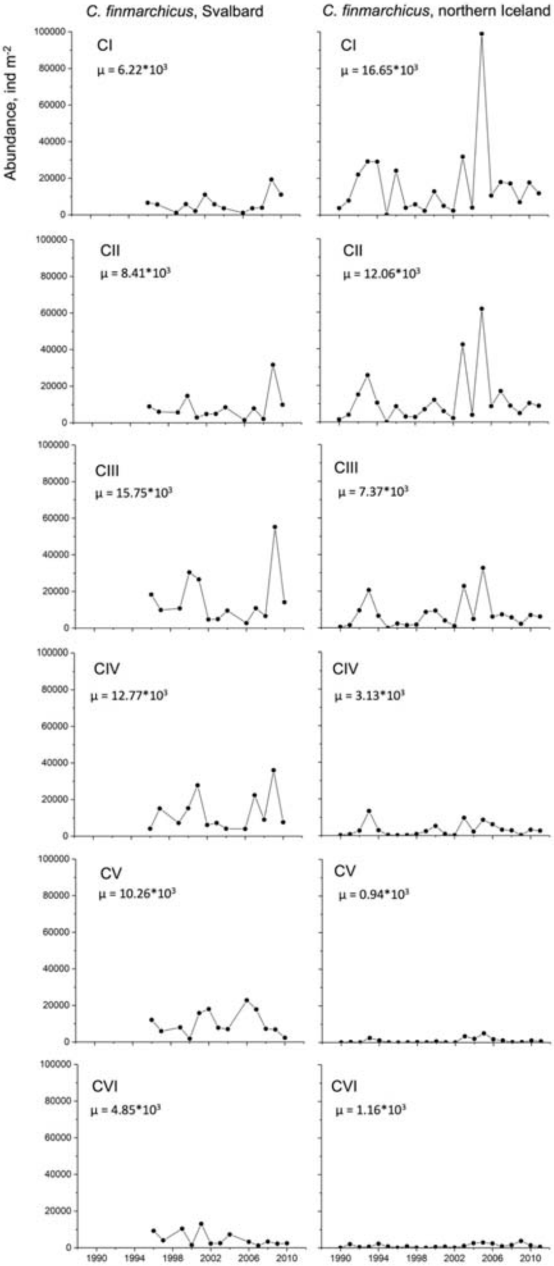
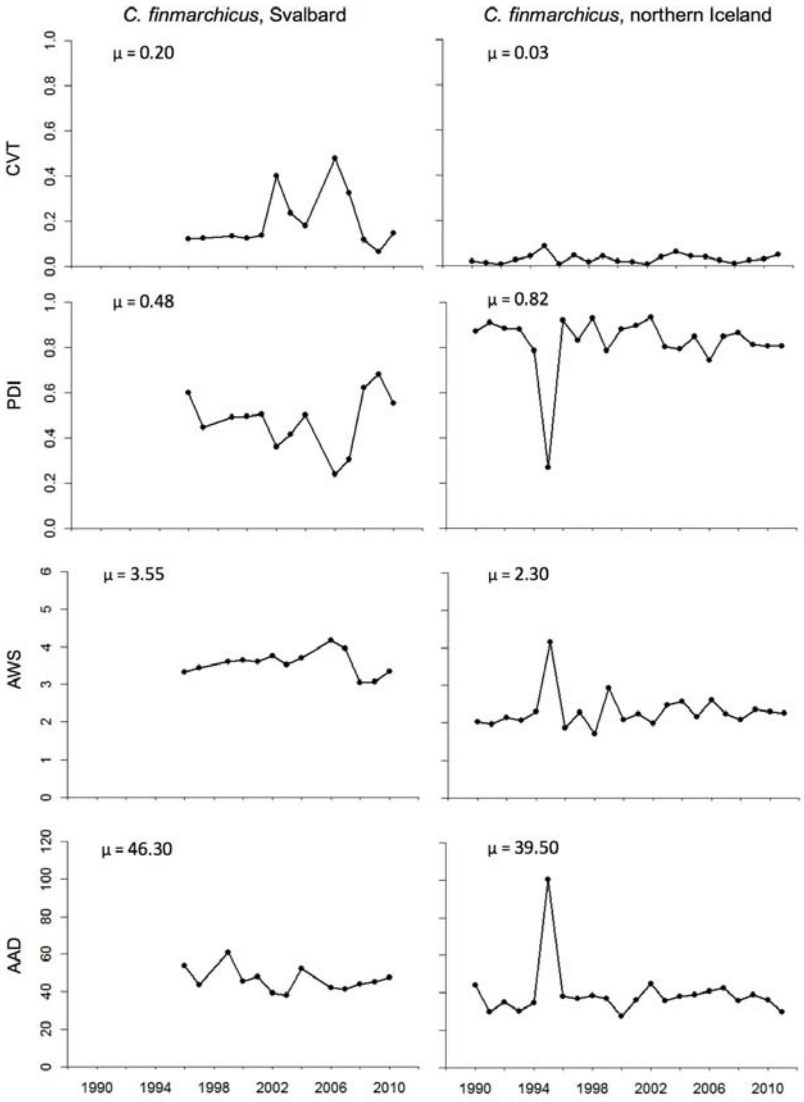

(a)
Svalbard
Northern Iceland
The start day of the spring bloom
180
170
160
150
140
130
120
(b)
Chl a concentration (mg L^{-1})
14
12
10
8
6
4
2
0
1990
1994
1998
2002
2006
2010

Fig. 4



C. finmarchicus, Svalbard
C. finmarchicus, northern Iceland
Abundance, ind m^{-2}
CI
μ = 6.22*10^3
CI
μ = 16.65*10^3
CII
μ = 8.41*10^3
CII
μ = 12.06*10^3
CIII
μ = 15.75*10^3
CIII
μ = 7.37*10^3
CIV
μ = 12.77*10^3
CIV
μ = 3.13*10^3
CV
μ = 10.26*10^3
CV
μ = 0.94*10^3
CVI
μ = 4.85*10^3
CVI
μ = 1.16*10^3
100000
80000
60000
40000
20000
0
1990
1994
1998
2002
2006
2010

Fig. 5



C. finmarchicus, Svalbard
C. finmarchicus, northern Iceland
CVT
PDI
AWS
AAD
μ = 0.20
μ = 0.03
μ = 0.48
μ = 0.82
μ = 3.55
μ = 2.30
μ = 46.30
μ = 39.50
0.0
0.2
0.4
0.6
0.8
1.0
0
1
2
3
4
5
6
0
20
40
60
80
100
120
1990
1994
1998
2002
2006
2010

Paper IV

Short communication

A vertical life table approach to copepod phenology: a comparison with horizontal approaches based on *Calanus glacialis* abundance time series in the White Sea, Russia

Marina Espinasse[1], Claudia Halsband[2], Øystein Varpe[2,3], Daria Martynova[4], Nikolay Usov[4], Ketil Eiane[1]

[1]Faculty of Biosciences and Aquaculture, Nord University, P.O Box 1490, NO-8049 Bodø, Norway,

[2]Akvaplan-niva, Fram Centre, P.O. Box 6606 Langnes, N-9296 Tromsø, Norway

[3] The University Centre in Svalbard (UNIS), P.O. Box 156, N-9171 Longyearbyen, Norway

[4] Zoological Institute of the Russian Academy of Sciences, Universitetskaya nab.1,

St. Petersburg 199034, Russia

Corresponding author: Marina Espinasse

E-mail: ecologM@hotmail.com

Abstract

Studies on *Calanus* spp. phenology are an important contribution to the understanding of phenology-environment relationships and the functioning of pelagic ecosystems under environmental fluctuations. The availability of data allowing to study annual *Calanus* population development across each stage of their life cycle (horizontal phenological indices) is limited, but seasonal data sets with information on only a few stages can also be used to calculate phenological proxies. This method is implemented in vertical life table approach to study zooplankton phenology. We investigate the suitability of the phenological indices based on the vertical life table approach for characterization of *Calanus* phenology. We compare vertical and horizontal phenological indices estimated for a six decades-long *Calanus glacialis* data series in the White Sea. We describe the correlations between the two approaches and discuss the limitations of vertical phenological indices. The results of the study suggest that vertical phenological indices correspond to horizontal phenological indices during the reproduction and growth season of *Calanus* (spring and summer) and show more correlations with environmental variables than horizontal indices.

Introduction

Shifts in phenology, the timing of life-history events, such as sexual maturity, spawning, and hibernation, can be the main effect of environmental variability on zooplankton populations (Edwards and Richardson, 2004). Climate variability may lead to alterations in seasonality and trophic interactions of plankton, and these changes can propagate to upper trophic levels (Hays et al., 2005). Studies of zooplankton phenology may, therefore, help to elucidate the mechanisms linking pelagic community responses to environmental variability (Ji et al., 2010).

Most phenology studies rely on indices of phenology estimated by a horizontal life table approach (Aksnes et al., 1997). This approach utilizes long-term stage- or age-structured data-series with temporal resolution that cover the entire life cycle of the organism under study (Batten and Mackas, 2009, Edwards and Richardson, 2004). Unfortunately, such data sets remain scarce for high latitude marine zooplankton. An alternative, but less explored approach in zooplankton phenology studies is to develop phenological indices by a so-called vertical life table approach (Aksnes et al., 1997). This approach utilizes "snapshots" of population age or stage-structure that cover a limited period each year over several years (e.g. Head et al., 2003, Mackas et al., 2007, Espinasse et al. in prep). It remains unclear, however, how these different approaches to phenology compare when applied to marine zooplankton.

In North Atlantic waters, calanoid copepods of the genus *Calanus* are the most ecologically important species, as they represent a key link between new production and higher trophic levels (Wassmann et al., 2006). Climatic fluctuations tend to alter *Calanus* phenology (Wilson et al., 2016, Head et al., 2013). Changes in *Calanus* phenology may reduce the temporal overlap with their higher trophic level predators (Cushing, 1990), thereby affecting energy flow in pelagic ecosystems (Falk-Petersen et al., 2007).

C. glacialis is mainly an Arctic water-associated species, which is found in the Arctic shelf areas and to a lesser extent, in the northern North Atlantic (Hirche and Kwasniewski, 1997, Conover, 1988). In the White Sea, *C. glacialis* has a two-year life cycle. During the first year, *C. glacialis* develops to copepodite stage CIV, which is the first overwintering stage. During the second year, CIV develops into a second overwintering stage CV. Maturation of the stage CV into adults usually occurs in spring, and spawning takes place from May to June (Kosobokova, 1999)

Here, we apply both horizontal and vertical life table approaches to a long-term data series on *C. glacialis*. We aim to compare the two approaches by investigating their interrelationships and responses to environmental variability, thereby shedding new light on the applicability of vertical phenological indices to studies of *Calanus* ecology.

Material and methods

Data set

We based our study on stage-structured abundance data of *C. glacialis* population in the White Sea in north-western Russia. Zooplankton was collected by the Zoological Institute of the Russian Academy of Sciences at one station (64 m depth; 66.32 °N; 33.67 °E; Fig.1) from 1961 to 2010 approximately every 10 days during the ice-free period (June to October) and otherwise approximately every month. Samples were collected with a Juday net (0.1 m^2 mouth area and 200 µm mesh size) from three depth bins (64 – 25 m, 25 – 10 m, 10 m – surface). *C. glacialis* was staged (nauplii, copepodite stages 1 through 5 (CI – CV), adult males and females), counted, and abundance estimates (ind m^{-2}) were calculated for each sampling day by summing over three depth intervals assuming 100% filtering efficiency of the net. We based our analysis on the abundances of copepodite stages and adults only, because the relatively coarse mesh size of the used plankton net implies that there may be sampling bias against the smaller stages.

As proxies for environmental variability we used water column temperature and salinity, as well as climate indices. Water temperature was measured by a bathythermograph GM7-III (USSR) or by reversing thermometers mounted on the bathometer BM-48 (USSR) at standard depths (0, 5, 10, 15, 25, 50, and 62 or 64 m) from 1990 to 2006. Conductivity was measured with a conductometer GM-65M (USSR), and salinity was calculated using standard tables (International Oceanographic Tables, 1981). From 2006 onwards, water temperature and salinity were measured by a CTD probe MIDAS 500 (Valeport Ltd.) from near the sea bed to the surface. We used depth averaged (0-64 m) temperature and salinity in testing for relationships between phenology indices and environmental variability.

As a proxy for climate variability during the study period we used the annual North Atlantic Oscillation index (NAO; www.climatedataguide.ucar.edu) and the annual Arctic Oscillation index (AO), calculated from the monthly indices downloaded from www.cpc.noaa.gov/.

Phenological indices

Phenological variability may be manifested differently over a life cycle, but there is no way of knowing *a priory*, when effects become apparent. Therefore, it is suggested to apply several phenological indices in one study (Thackeray et al., 2012). Thus, we based our analysis on seven phenological indices developed from the stage-structured abundance data of *C. glacialis*. Four of these indices were developed as a vertical life table approach and three were horizontal phenological indices. The indices were selected so as to reflect phenological effects at different stages of the life cycle of *C. glacialis* such as reproduction, recruitment to copepodites, and the onset of hibernation.

To reflect phenological variability occurring in late developmental stages, we used the proportion of copepodite stage V (CV) to total copepodite abundance (CVT) according to Mackas et al. (1998, 2007) as

$$CVT = \frac{N_{CV}}{N_{tot}} \tag{1}$$

where N_{CV} is the abundance of stage CV, and N_{tot} is the total abundance of *Calanus* copepodites in the sample. CVT takes values from 0 (no CVs in the population) to 1 (population consists only of CVs).

To focus on phenology of the earlier parts of the life-cycle, we used the population development index (PDI), defined as the numerical proportion of early copepodite stages (CI to CIII) to total abundance of copepodites (Head et al. 2013, 2003),

$$PDI = \frac{N_{CI-CIII}}{N_{tot}} \tag{2}$$

where $N_{CI-CIII}$ is the sum of the abundances of copepodite stages CI to CIII and N_{tot} is the total abundance of copepodites.

The average weighted stage (AWS) of the population, is a more integrated measure of phenology that should be able to capture phenological effects on all parts of the life cycle.

$$AWS = \frac{\sum_{k=1}^{6} (N_k * k)}{\sum_{k=1}^{6} N_{tot}} \tag{3}$$

where k is the ranked order of copepodite stages (CI = 1, CII = 2, etc) and N_k is the abundance of copepodite stage k in the sample.

Similarly, we used the average age in days (AAD) of the population as

$$AAD = \frac{\sum_{k=1}^{6}(D_k * x)}{\sum_{k=1}^{6} x} \quad (4)$$

where x is the abundance of each ranked copepodite stage in a sample, and D_k is an estimated age (days) of copepodite stage k. D_k was estimated from the function relating *C. finmarchicus* development to ambient temperature (T) at the time of sampling as

$$D = a(T - \alpha)^{-2.05} \quad (5)$$

(McLaren 1978) where a and α are empirically fitted constants (Campbell et al., 2001). The conversion of development times of *C. finmarchicus* to development times of *C. glacialis* was done as described in Arnkværn et al. (2005). The index AAD, contrary to the other vertical indices, incorporates a link to environmental variability (temperature), which is extrinsic to the population.

We compared and contrasted the behaviour of the abovementioned vertical life table indices with the three indices developed as a horizontal approach. First, to focus on the older life stages, we used the day of year when the proportion of developmental stage CIV reached ≥ 0.80 of the total population each year (Peak CIV). We restricted the calculation of this index to days of a year > 150 to limit the influence of overwintered CIVs in the estimates, because the pool of overwintered CIVS is largely depleted by this time (Kosobokova 1999). This index is a modification of the peak biomass index used by Mackas et al. (1998, 2007) for *Neocalanus plumchrus* populations in the Pacific Ocean. We chose to focus on the developmental stage CIV, instead of CVs, as (Mackas et al., 2007, 1998) did, because this is the predominant *C. glacialis* overwintering stage in the White Sea (Prygunkova, 1968). Thus, Peak CIV likely indicates the end of the growth season and marks the onset of hibernation during the first year of *C. glacialis* life cycle in the White Sea.

Secondly, we used the appearance of CIs (ACI) (Usov et al., 2013), the ten-day period each year when the abundance of copepodite stage CI exceed 10% of the total *C. glacialis* abundance, as this index likely captures the timing of reproduction and the variability in early life stages.

Finally, as a more integrated index, potentially sensitive to variability in all developmental stages, we used the centre of gravity index (CGI) of Edwards and Richardson (2004)

$$CGI = \frac{\sum_{m=1}^{12} m * x_m}{\sum_{m=1}^{12} x_m} \quad (7)$$

where m is the order of months of a year (January = 1, February = 2, etc.) and x_m is the mean abundance (all copepodite stages) of *C. glacialis* in month m.

Relationships between phenological indices and between phenological indices and environment

To quantify seasonal variability in the relationship between vertical and horizontal phenological indices, we correlated monthly values (March through August) of the vertical phenological indices with yearly horizontal indices. We restricted our analysis to spring and summer months because *C. glacialis* overwinters at depths > 200 m in the White Sea (Pertsova and Kosobokova, 2010) and thus, can be underestimated in our shallow station (64 m) during autumn and winter.

To test for how the phenology indices responded to environmental variability, we correlated indices with proxies of environmental variability. Monthly vertical phenological indices (March to August) were correlated with water column temperature and salinity of the same month, as well as with annual NAO and AO indices. As AAD is a function of temperature, we did not correlate this index against temperature. Horizontal indices were correlated with water column temperature and salinity in spring (May), because environmental conditions in spring are critical for the early development of *C. glacialis* in the White Sea (Pertsova and Kosobokova 2010: Usov 2015). In the White Sea, spring is defined as a time when water column temperature exceeds 0 °C (Usov et al., 2013), and in our data set, this usually occurred in May. Horizontal indices were also correlated with annual NAO and AO indices.

Phenological indices deviated from the Gaussian distribution and some also contained outliers, thus, all correlations were calculated with a Kendall's rank correlation test (Kendall, 1970). Due to multiple correlations performed, we corrected the threshold p-value following Benjamini and Hochberg (1995). Only correlations that remained significant after the correction were reported.

Results

Environmental variability

Average spring (May) temperature (0-64 m) in the White Sea varied mainly between 0 and 1°C. Especially cold years were 1971 (-0.82°C) and 1981 (-0.79°C; Fig.2), while 2007 was unusually warm (1.54°C). Temperature increased over the time series (linear regression: T= 0.012*year -24.5, $R^2 = 0.13$, $p = 0.011$, $df = 38$). Salinity varied around 28 psu, but in 1979 and 2003, salinity decreased to just above 25 psu (Fig. 2). No temporal trend was identified for salinity in May.

Phenological indices

Seasonal patterns in the vertical phenological indices were largely repeated between years (Fig. 3). CVT peaked between April and early June, and again in December. The peak of PDI usually occurred about a month after the peak in CVT, from early June to the middle of July. AWS decreased towards June and July and increased thereafter, while, AAD remained high in January through April, and decreased towards minimum in June and July and then increased again (Fig. 3).

The day of the peak abundance of CIV (Peak CIV) varied from day 182 (end of June) to day 232 (August). Peak CIV was earliest in the season in 1968 and 1995, and latest in 1969 and 1998 (Fig.4). This index showed a sharp increase from 1996 to 1998 (from 182 to 232), but was less variable in the other years. The appearance of CI (ACI) varied from day 130 (early May) to day 200 (mid-July) and was earliest in 2006 and 2007, while latest in 1966. The amplitude of variation in ACI was generally smaller, and in some periods (e.g. 1975 to 1977) remained constant between years. The centre of gravity index (CGI) varied between 5.5 and 7.7 and was lowest in 1962 and 2010, while the highest values of this index were observed in 1971 and 2005. Year-to-year fluctuations in CGI were larger at the beginning of the time-series, when it increased from 5.7 in 1962 to 7.2 in 1963, and at the end of the time-series when the index decreased from 7.2 in 2009 to 5.5 in 2010.

Comparison of the vertical and horizontal indices

All vertical phenological indices correlated with at least one of the horizontal indices (Table I). CVT correlated negatively with CGI in July (Table I). PDI correlated positively with Peak CIV in July and correlated negatively with ACI in May, and positively in July.

AWS correlated negatively with Peak CIV in July, positively with ACI in May and negatively with ACI in July. AAD correlated positively with both ACI and CGI in May.

The relationship between phenological indices and environmental variability

All the vertical phenological indices correlated with either temperature or salinity (Table II), but only in one case (AAD), did we detect a correlation with climate variability (AO). CVT correlated positively with temperature in June but negatively with temperature in July and with salinity in April. PDI correlated positively with temperature in May and June but negatively with temperature in July. AWS correlated negatively with temperature in May, and AAD correlated with salinity in July and August.

Among the horizontal phenology indices, only ACI and CGI correlated with environmental variability (Table III). In both cases, there was a negative relationship with temperature in May.

Discussion

Comparison between vertical and horizontal phenological indices

Our results indicated that there was a fair degree of correlation between phenological indices based on vertical and horizontal approaches (Table I). In all cases, significant correlations occurred in spring or summer (May, July), which coincides with the seasonal peak of young copepodite stages, and also with the peak of total abundance of *C. glacialis* in the White Sea (Kosobokova 1999). These correlations between vertical and horizontal phenological indices indicate that both approaches are able to identify phenology signals.

More correlations were found between vertical indices and environmental variables than between horizontal indices and environment. Two of the three horizontal indices (Appearance of CI - ACI, centre of gravity index - CGI) were related to temperature (Table III). In contrast, all vertical indices were related to environmental variability. Most were related to the variability in water column temperature or salinity, and in one case (AAD), to climate variability (AO) (Table II). Therefore, phenological indices based on a vertical life table approach were at least as sensitive for the detection of environment-phenology relationships as horizontal indices (Usov et al., 2013, Edwards and Richardson, 2004, Mackas et al., 2012).

Phenology indices and *C. glacialis* ecology

In spring, copepodites CVI of *C. glacialis* migrate to the surface water layers to molt into CV, and by June, the bulk of the second-year cohort is represented by CVs (Prygunkova, 1968, Kosobokova, 1999). However, in cold years in the White Sea, spring temperatures are low (such as in 1964, 1969, 1971, 1981; Fig.2), and the warming of the surface water layers is relatively slow (Babkov and Lukanin, 1985). In these conditions, the development of the overwintered CIVs into CVs can be delayed (Pertsova and Kosobokova, 2010), resulting in lower CVT in July in cold years. This effect is also reflected in our study by the correlation between temperature in June and CVT (Table II), implying that higher temperatures during the development of CIV into CV (May, June) increased abundances of CV in early summer.

Similarly, spawning and development of eggs and nauplii is usually delayed in cold years (Pertsova and Kosobokova, 2010) and thus, the recruitment to early copepodite stages occurs later in the season than in warmer years. The peak of total abundance of *C. glacialis* in the White Sea coincides with early growth season (Pertsova and Kosobokova 2010), and delayed spawning and growth are reflected in a later than usual abundance peak, and thus, in a relatively high CGI in cold years (Figs.4). The opposite situation occurs in warmer years, when early onset of spawning results in an earlier abundance peak and lower CGI.

Recruitment of the new copepodite generation (CI to CIII) occurs relatively early in spring in warm years (such as 1983, 2006, 2007 in our study; Fig. 2), and most copepodites reach the first overwintering stage (CIV) by late July in such years (Kosobokova and Pertsova 2010). Therefore, the proportion of early copepodites (PDI) was relatively low in July in warm years, since recruitment occurred early in spring (low ACI). In contrast, AWS and AAD remained high in July in those years, because they also reflect the abundances of older copepodite stages. This explains the positive relationship between PDI and ACI in July in warm years, while negative relationship between ACI and AWS (Table I).

The timing of spawning event of *C. glacialis* may vary by several weeks in the White Sea, but usually occurs between May and June (Pertsova and Prygunkova, 1995). Accordingly, the timing of recruitment to early copepodites and overwintering stages vary interannually. The positive association between AAD and CGI, probably reflected interannual shifts in the timing of recruitment of the new *C. glacialis* generation into copepodites. Early spawning followed by an earlier recruitment implied relatively low AAD in May, because of increasing proportion of CIs in the population, and consequently, the peak of population abundance (as indicated by CGI), may have occured as early as in mid-May (Fig. 4).

Correlations between ACI and PDI, AWS and AAD in spring (May) were different from those observed in July (Table I). This was likely because in warm years, when the appearance of CIs occurred early (i.e., low ACI years), *C. glacialis* population in May consisted largely of early copepodite stages (CI – CIII). Later spawning, in contrast, would imply that some nauplii have not yet recruited into early developmental stages by the end of May (Pertsova and Kosobokova 2010), contributing to a lower PDI in cold years. This explains, why the May correlation between ACI and PDI was negative, while positive between ACI and AWS and between ACI and AAD.

Overall, vertical indices appeared to be more related to the horizontal index ACI, which indicates the timing of spawning and early development of *C. glacialis* copepodites in the White Sea (Usov et al., 2013). Fewer correlations were established with Peak CIV, which is more related to phenology changes occurring near the end of the developmental season. We interpret this as a stronger relationship between vertical and horizontal phenological indices during reproduction and early growth season of *C. glacialis*.

At the same time, the seasonal variation of all four vertical indices decreased towards the end of the growth season in August (Fig. 3) and was minimal during overwintering season. Decreased variability of the vertical phenological indices during overwintering may suggest that they are less affected by environmental variability at this period. This finding has implications for the use of the vertical phenological indices for *Calanus* abundance data – they appear to convey more information on phenological variability in *Calanus* outside the overwintering season.

As the present study was based on a *C. glacialis* with a two-year life cycle, the applicability of the index CVT may be more limited compared to the applicability of this index for species with a shorter generation time. In the White Sea, CV is a second overwintering stage, which appears in surface waters in spring, at the same time as the overwintered CIV moult into CVs (Prygunkova et al., 1968). The two cohorts of CVs may therefore occasionally overlap in the White Sea in spring (own observations). Thus, CVT should be interpreted with caution when applied to spring abundance data of *Calanus* populations with a several-years life span, because in this case, CVT may reflect differences in the abundances of the two consecutive cohorts of CVs rather than phenological variability as such.

We conclude that the vertical life table approach is a useful tool in studies of phenological variability in *Calanus*. The revealed limitations of the vertical phenological indices are limited applicability during overwintering season of *Calanus*, and a potential overlap of the different cohorts of overwintering copepodites CV in phenological estimation based on spring data.

References

Aksnes, D.L., Miller, C.B., Ohman, M.D. & Wood, S.N. (1997). Estimation techniques used in studies of copepod population dynamics - A review of underlying assumptions. *Sarsia,* 82**:** 279-296.

Arnkvaern, G., Daase, M. & Eiane, K. (2005). Dynamics of coexisting *Calanus finmarchicus*, *Calanus glacialis* and *Calanus hyperboreus* populations in a high-Arctic fjord. *Polar Biol,* 28**:** 528-538. DOI 10.1007/s00300-005-0715-8

Babkov, A.I. & Lukanin, V.V. (1985). Spring alterations of salinity and temperature of surface waters of the White Sea and its influence of the distribution of littoral and sublittoral organisms. *Biocenoses of the Chupa Inlet of the White Sea and their seasonal dynamics Issledovaniya fauni morei 31(39).* Leningrad: Nauka.

Batten, S.D. & Mackas, D.L. (2009). Shortened duration of the annual Neocalanus plumchrus biomass peak in the Northeast Pacific. *Mar Ecol Prog Ser,* 393**:** 189-198. DOI 10.3354/meps08044

Benjamini, Y. & Hochberg, Y. (1995). Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing. *Journal of the Royal Statistical Society Series B (Methodological),* 57**:** 289-300.

Conover, R.J. (1988). Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the northern hemisphere. *Hydrobiologia,* 167/168**:** 127-142.

Cushing, D.H. (1990). Plankton Production and Year-class Strength in Fish Populations: an Update of the Match/Mismatch Hypothesis. IN Blaxter, J.H.S. & Southward, A.J. (Eds.) *Adv Mar Biol.* Academic Press.

Edwards, M. & Richardson, A.J. (2004). Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature,* 430**:** 881-884.

Falk-Petersen, S., Pavlov, V., Timofeev, S. & Sargent, J. (2007). Climate variability and possible effects on arctic food chains: The role of Calanus. IN Ørbæk, J., Kallenborn, R., Tombre, I., Hegseth, E., Falk-Petersen, S. & Hoel, A. (Eds.) *Arctic Alpine Ecosystems and People in a Changing Environment.* Springer Berlin Heidelberg.

Hays, G.C., Richardson, A.J. & Robinson, C. (2005). Climate change and marine plankton. *Trends Ecol Evol,* 20**:** 337-344. DOI 10.1016/j.tree.2005.03.004

Head, E.J.H., Harris, L.R. & Yashayaev, I. (2003). Distributions of Calanus spp. and other mesozooplankton in the Labrador Sea in relation to hydrography in spring and summer (1995–2000). *Prog Oceanogr,* 59**:** 1-30. DOI 10.1016/S0079-6611(03)00111-3

Head, E.J.H., Melle, W., Pepin, P., Bagøien, E. & Broms, C. (2013). On the ecology of Calanus finmarchicus in the Subarctic North Atlantic: A comparison of population dynamics and environmental conditions in areas of the Labrador Sea-Labrador/Newfoundland Shelf and Norwegian Sea Atlantic and Coastal Waters. *Prog Oceanogr,* 114**:** 46-63. DOI 10.1016/j.pocean.2013.05.004

Hirche, H.-J. & Kwasniewski, S. (1997). Distribution, reproduction and development of Calanus species in the Northeast water in relation to environmental conditions. *J Mar Syst,* 10**:** 299-317. DOI 10.1016/S0924-7963(96)00057-7

Ji, R., Edwards, M., Mackas, D.L., Runge, J.A. & 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

Kendall, M.G. (1970). *Rank correlation methods,* London: Griffin.

Kosobokova, K.N. (1999). The reproductive cycle and life history of the Arctic copepod *Calanus glacialis* in the White Sea. *Polar Biol,* 22**:** 254-263. DOI 10.1007/s003000050418

Mackas, D.L., Batten, S. & Trudel, M. (2007). Effects on zooplankton of a warmer ocean: Recent evidence from the Northeast Pacific. *Prog Oceanogr,* 75**:** 223-252. DOI 10.1016/j.pocean.2007.08.010

Mackas, D.L., Goldblatt, R. & Lewis, A.G. (1998). Interdecadal variation in developmental timing of Neocalanus plumchrus populations at Ocean Station P in the subarctic North Pacific. *Can J Fish Aquat Sci,* 55**:** 1878-1893. DOI 10.1139/f98-080

Mackas, D.L., Greve, W., Edwards, M., Chiba, S., Tadokoro, K., Eloire, D., Mazzocchi, M.G., Batten, S., Richardson, A.J., Johnson, C., Head, E., Conversi, A. & Peluso, T. (2012). Changing zooplankton seasonality in a changing ocean: Comparing time series of zooplankton phenology. *Prog Oceanogr,* 97-100**:** 31-62. DOI 10.1016/j.pocean.2011.11.005

Pertsova, N.M. & Kosobokova, K.N. (2010). Interannual and seasonal variation of the population structure, abundance, and biomass of the arctic copepod Calanus glacialis in the White Sea. *Oceanology,* 50**:** 531-541. DOI 10.1134/s0001437010040090

Pertsova, N.M. & Prygunkova, R.V. (1995). Zooplankton. IN Berger, V.J. (Ed.) *White Sea Biological resources and problems of their rational epxploitation.* St. Petersburg: Zoological Institute publisher.

Prygunkova, R.V. (1968). On the cycle of development of *Calanus* (*Calanus glacialis* Jaschnov) in the White Sea (In Russian). *Doklady Akademii Nauk USSR,* 182**:** 1447-1450.

Thackeray, S.J., Henrys, P.A., Jones, I.D. & Feuchtmayr, H. (2012). Eight decades of phenological change for a freshwater cladoceran: what are the consequences of our definition of seasonal timing? *Freshwat Biol,* 57**:** 345-359. DOI 10.1111/j.1365-2427.2011.02614.x

Usov, N. (2015). Seasonal and long-term dynamics of zooplankton abundances in the coastal zone of Kandalaksha Bay, White Sea, in relation to temperature fluctuations. PhD dissertation (In Russian). Saint-Petersburg: Zoological Institute of the Russian Academy of Sciences.

Usov, N., Kutcheva, I., Primakov, I. & Martynova, D. (2013). Every species is good in its season: Do the shifts in the annual temperature dynamics affect the phenology of the zooplankton species in the White Sea? *Hydrobiologia,* 706**:** 11-33. DOI 10.1007/s10750-012-1435-z

Wassmann, P., Reigstad, M., Haug, T., Rudels, B., Carroll, M.L., Hop, H., Gabrielsen, G.W., Falk-Petersen, S., Denisenko, S.G., Arashkevich, E., Slagstad, D. & Pavlova, O. (2006). Food webs and carbon flux in the Barents Sea. *Prog Oceanogr, 71***:** 232-287. DOI 10.1016/j.pocean.2006.10.003

Wilson, R.J., Banas, N.S., Heath, M.R. & Speirs, D.C. (2016). Projected impacts of 21st century climate change on diapause in *Calanus finmarchicus*. *Global Change Biol***,** 22: 3332-3340. DOI 10.1111/gcb.13282

Tables

Table I. Significant correlations between monthly (March to August) vertical phenological indices and horizontal phenological indices. Month denotes the selected period for the estimates of the vertical phenological indices. CVT is the proportion of copepodites CV to total abundance; PDI is the population development index; AWS is average weighted stage; AAD is average age in days; Peak CVI is the day of the peak abundance of copepodites CIV; ACI is the day of the appearance of copepodites CI; CGI is the centre of gravity index; τ is Kendall's tau correlation, *P* is the p-value of the correlation test; *df* denotes degrees of freedom

Vertical index	**Horizontal index**	**Month**	τ	***P***	***df***
CVT	CGI	July	-0.22	<0.001	158
PDI	Peak CIV	July	0.32	<0.001	152
	ACI	May	-0.34	0.0002	76
		July	0.36	<0.001	142
AWS	Peak CVI	July	-0.24	<0.001	152
	ACI	May	0.25	0.002	76
		July	-0.29	<0.001	142
AAD	ACI	May	0.32	0.0002	75
	CGI	May	0.28	0.0002	74

Table II. Significant correlations between monthly (March to August) vertical phenological indices and environmental variables. T and S denote average water temperature and salinity (0-64 m), AO denotes annual Artic Oscillation index, and other symbols are as defined in Table I

Vertical index	Environmental variable	Month	τ	*P*	*df*
CVT	T	June	0.37	<0.001	133
		July	-0.18	<0.001	154
	S	April	-0.33	<0.001	65
PDI	T	May	0.44	<0.001	77
		June	0.20	0.001	133
		July	-0.25	<0.001	154
AWS	T	May	-0.22	0.004	77
AAD	S	July	0.16	0.003	149
	S	Aug	0.22	<0.001	136
	AO	June	-0.15	0.008	133

Table III. Significant correlations between horizontal phenological indices and environmental variables. ACI is the day of the appearance of copepodites CI, CGI is the centre of gravity index. T is average water temperature (0-64 m) in May

Horizontal index	**Environmental variable**	τ	***P***	***df***
ACI	T	-0.44	<0.001	35
CGI	T	-0.42	<0.001	38

Figure legends

Figure 1. The location of the study area in the White Sea, Russia. WS indicate the location of the sampling station.

Figure 2. May temperature (upper panel) and salinity (lower panel) at the sampling station (0- 64 m) in the White Sea. The line in the upper panel represent a linear trend: T= 0.012*year -24.5, $R^2 = 0.13$, $p = 0.011$, $df = 38$.

Figure 3. Monthly means of the vertical phenological indices for *C. glacialis* abundance data in the White Sea in 1961-2010. Whiskers are 95% bootstrapped confidence intervals of mean values of the vertical indices each month. See text for details.

Figure 4. Horizontal indices for *C. glacialis* abundance data in the White Sea in 1961-2010. The abbreviations for horizontal phenological indices are as follows: Peak CIV – the day of the peak abundance of copepodites CIV; ACI – the day of the appearance of copepodites CI; CGI – centre of gravity index. See text for details.

Fig. 1

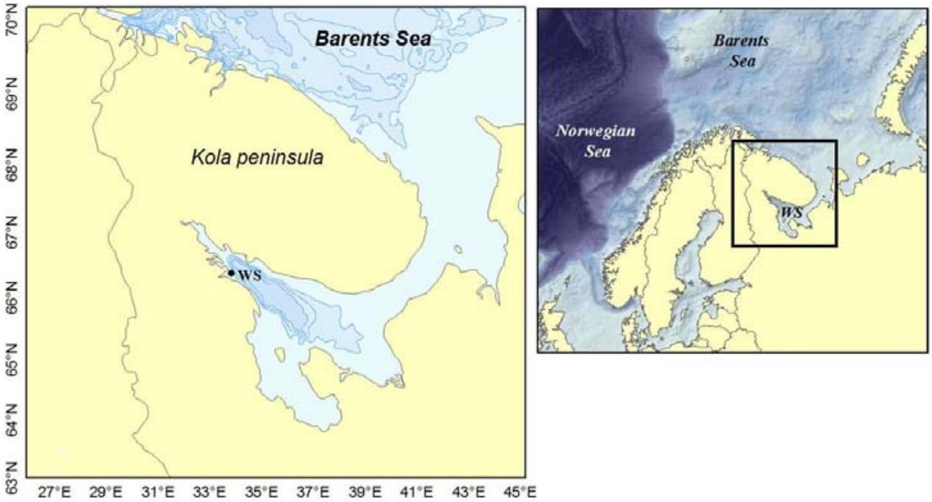

Barents Sea
Kola peninsula
WS
70°N
69°N
68°N
67°N
66°N
65°N
64°N
63°N
27°E
29°E
31°E
33°E
35°E
37°E
39°E
41°E
43°E
45°E
Barents Sea
Norwegian Sea
WS

Fig.2

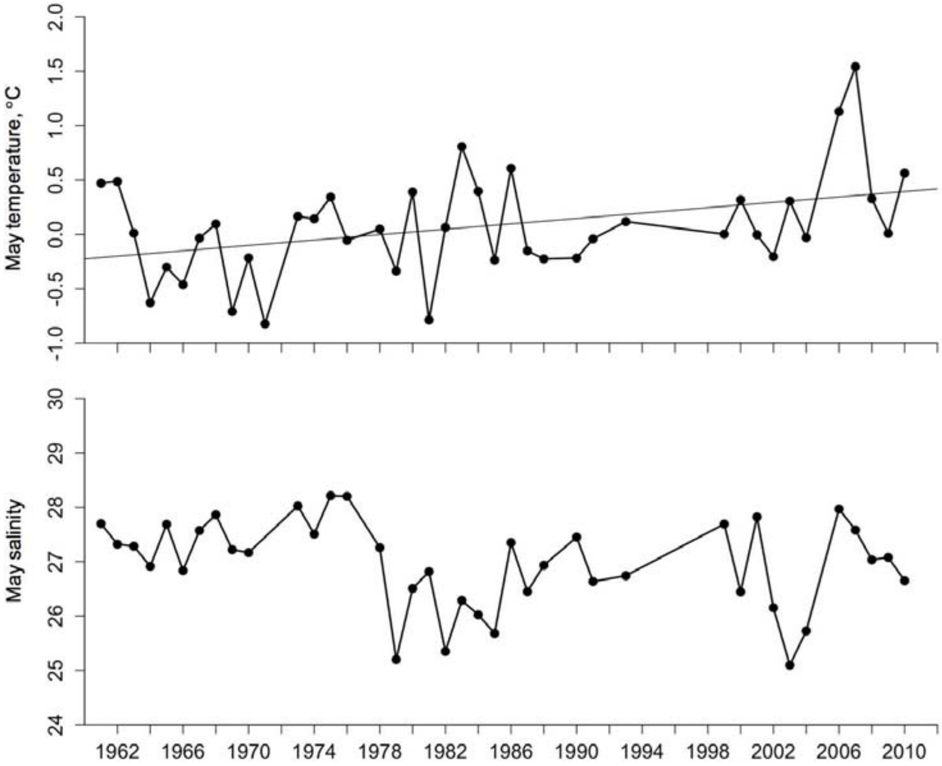

May temperature, °C
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
May salinity
30
29
28
27
26
25
24
1962
1966
1970
1974
1978
1982
1986
1990
1994
1998
2002
2006
2010

Fig. 3

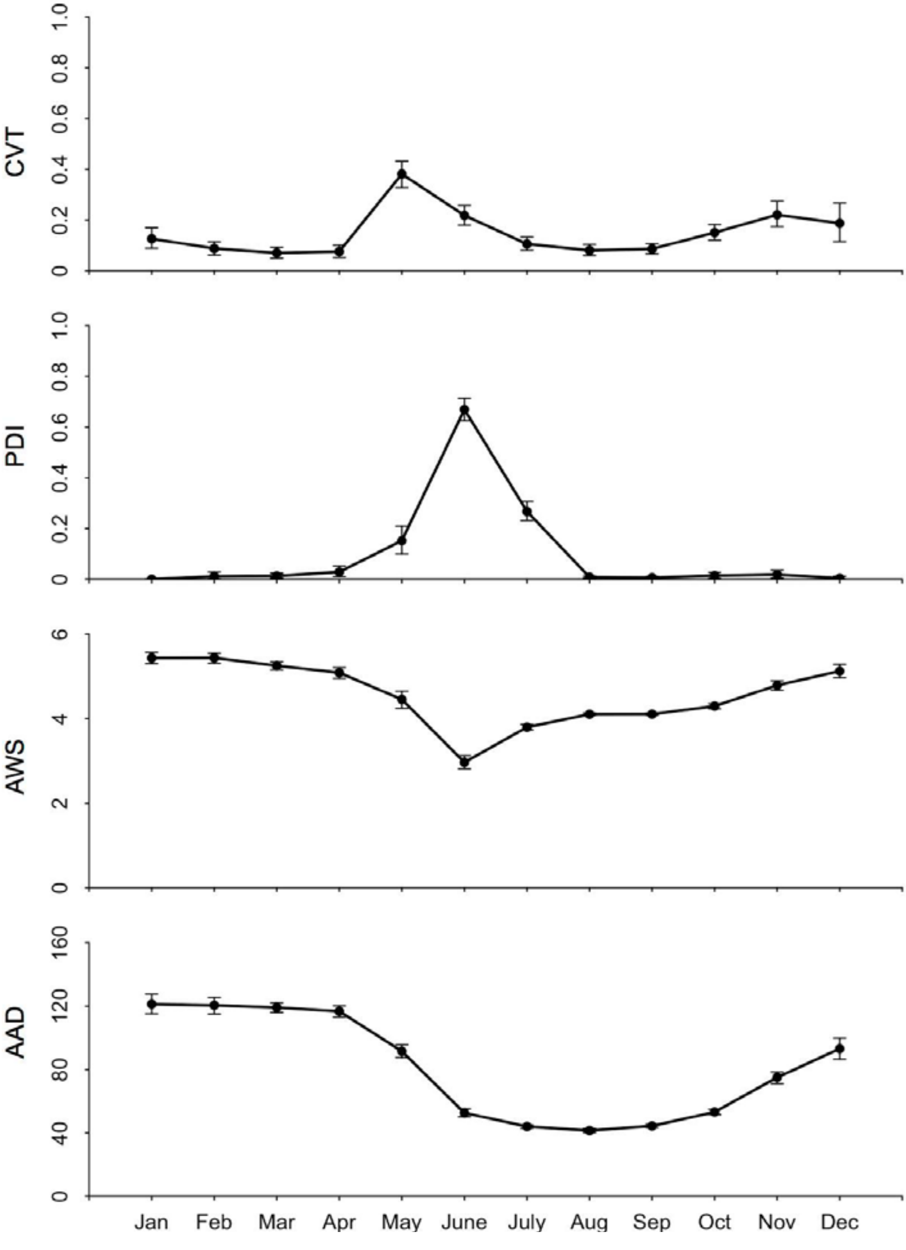
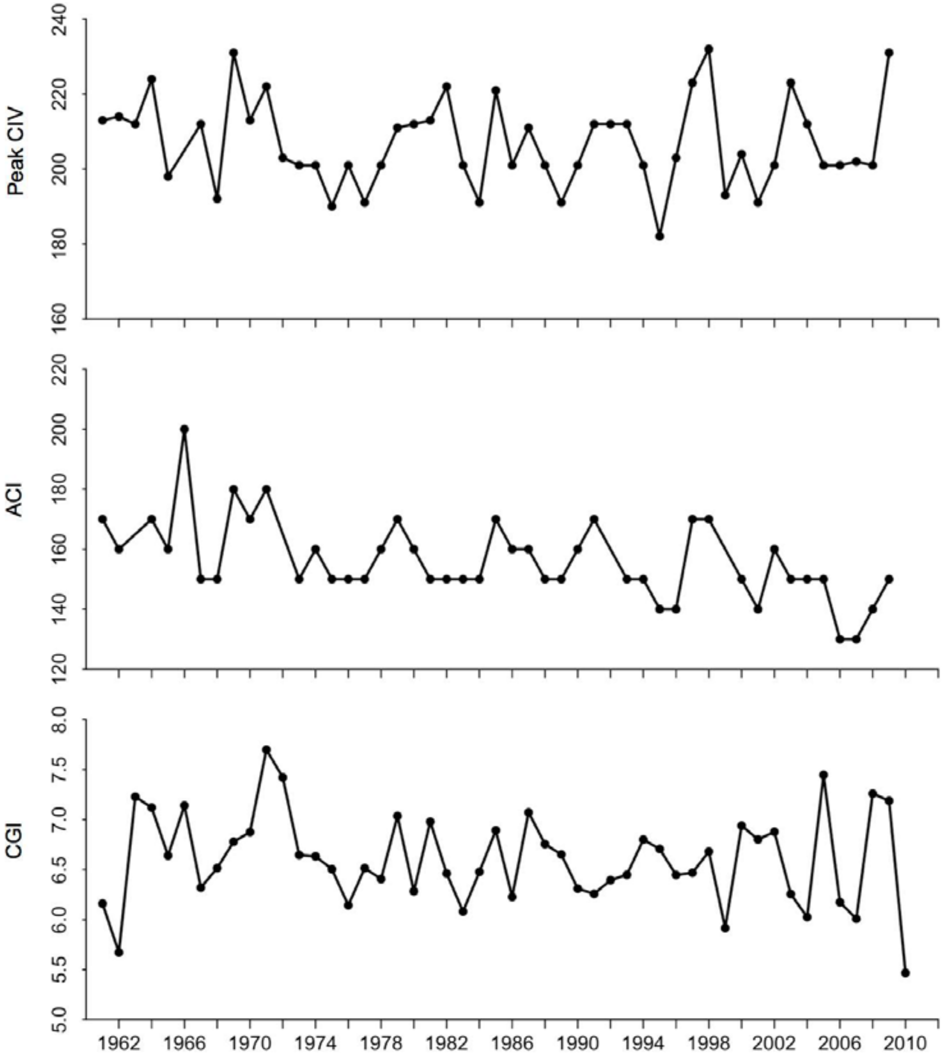

CVT
0
0.2
0.4
0.6
0.8
1.0
PDI
0
0.2
0.4
0.6
0.8
1.0
AWS
0
2
4
6
AAD
0
40
80
120
160
Jan
Feb
Mar
Apr
May
June
July
Aug
Sep
Oct
Nov
Dec

Fig.4


Peak CIV
160
180
200
220
240
ACI
120
140
160
180
200
220
CGI
5.0
5.5
6.0
6.5
7.0
7.5
8.0
1962
1966
1970
1974
1978
1982
1986
1990
1994
1998
2002
2006
2010

List of previously published theses for PhD in Aquaculture / PhD in Aquatic Biosciences,

Nord University

No. 1 (2011)
PhD in Aquaculture
Chris André Johnsen
Flesh quality and growth of farmed Atlantic salmon (*Salmo salar* L.) in relation to feed, feeding, smolt type and season
ISBN: 978-82-93165-00-2

No. 2 (2012)
PhD in Aquaculture
Jareeporn Ruangsri
Characterization of antimicrobial peptides in Atlantic cod
ISBN: 978-82-93165-01-9

No. 3 (2012)
PhD in Aquaculture
Muhammad Naveed Yousaf
Characterization of the cardiac pacemaker and pathological responses to cardiac diseases in Atlantic salmon (*Salmo salar* L.)
ISBN: 978-82-93165-02-6

No. 4 (2012)
PhD in Aquaculture
Carlos Frederico Ceccon Lanes
Comparative Studies on the quality of eggs and larvae from broodstocks of farmed and wild Atlantic cod
ISBN: 978-82-93165-03-3

No. 5 (2012)
PhD in Aquaculture
Arvind Sundaram
Understanding the specificity of the innate immune response in teleosts: Characterisation and differential expression of teleost-specific Toll-like receptors and microRNAs
ISBN: 978-82-93165-04-0

No. 6 (2012)
PhD in Aquaculture
Teshome Tilahun Bizuayehu
Characterization of microRNA during early ontogeny and sexual development of Atlantic halibut (*Hippoglossus hippoglossus* L.)
ISBN: 978-82-93165-05-7

No. 7 (2013)
PhD in Aquaculture
Binoy Rajan
Proteomic characterization of Atlantic cod skin mucosa – Emphasis on innate immunity and lectins
ISBN: 978-82-93165-06-04

No. 8 (2013)
PhD in Aquaculture
Anusha Krishanthi Shyamali Dhanasiri
Transport related stress in zebrafish: physiological responses and bioremediation
ISBN: 978-82-93165-07-1

No. 9 (2013)
PhD in Aquaculture
Martin Haugmo Iversen
Stress and its impact on animal welfare during commercial production of Atlantic salmon (*Salmo salar* L.)
ISBN: 978-82-93165-08-8

No. 10 (2013)
PhD in Aquatic Biosciences
Alexander Jüterbock
Climate change impact on the seaweed *Fucus serratus*, a key foundational species on North Atlantic rocky shores
ISBN: 978-82-93165-09-5

No. 11 (2014)
PhD in Aquatic Biosciences
Amod Kulkarni
Responses in the gut of black tiger shrimp *Penaeus monodon* to oral vaccine candidates against white spot disease
ISBN: 978-82-93165-10-1

No. 12 (2014)
PhD in Aquatic Biosciences
Carlo C. Lazado
Molecular basis of daily rhythmicity in fast skeletal muscle of Atlantic cod *(Gadus morhua)*
ISBN: 978-82-93165-11-8

No. 13 (2014)
PhD in Aquaculture
Joanna Babiak
Induced masculinization of Atlantic halibut (*Hippoglossus hippoglossus* L.): towards the goal of all-female production
ISBN: 978-82-93165-12-5

No. 14 (2015)
PhD in Aquaculture
Cecilia Campos Vargas
Production of triploid Atlantic cod: A comparative study of muscle growth dynamics and gut morphology
ISBN: 978-82-93165-13-2

No. 15 (2015)
PhD in Aquatic Biosciences
Irina Smolina
Calanus in the North Atlantic: species identification, stress response, and population genetic structure
ISBN: 978-82-93165-14-9

No. 16 (2016)
PhD in Aquatic Biosciences
Lokesh Jeppinamogeru
Microbiota of Atlantic salmon (*Salmo salar L.*), during their early and adult life
ISBN: 978-82-93165-15-6

No. 17 (2017)
PhD in Aquatic Biosciences
Christopher Edward Presslauer
Comparative and functional analysis of microRNAs during zebrafish gonadal development
ISBN: 978-82-93165-16-3

No. 18 (2017)
PhD in Aquatic Biosciences
Marc Jürgen Silberberger
Spatial scales of benthic ecosystems in the sub-Arctic Lofoten-Vesterålen basin
ISBN: 978-82-93165-17-0

No. 19 (2017)
PhD in Aquatic Biosciences
Marvin Choquet
Combining ecological and molecular approaches to redefine the baseline knowledge of the genus Calanus in the North Atlantic and the Arctic Oceans
ISBN: 978-82-93165-18-7

No. 20 (2017)
PhD in Aquatic Biosciences
Torvald B. Egeland
Reproduction in Arctic charr – timing and the need for speed
ISBN: 978-82-93165-19-4

The North Atlantic Ocean is a diverse and rich marine region, providing vast resources for modern fisheries. The functioning of this region is largely maintained by key zooplankton species, of which copepods of the genus *Calanus* are of particular significance. Changes in the distribution and abundance of *Calanus* spp. may have adverse consequences for pelagic food webs of the North Atlantic ecosystems. Therefore, it is important to build an understanding of what drives the variability in *Calanus* populations. Previous research has shown that *Calanus* distribution, abundance, and phenology (the timing of life cycle events) are affected by environmental variability acting on regional (e.g. climate) and more local (e.g. hydrography, circulation system, food availability) spatial scales. However, there is limited knowledge of the interplay and relative importance of local and large-scale environmental factors for the interannual variability of *Calanus* populations. In this dissertation, I aim to contribute to fill this knowledge gap by studying long-term data-series of *Calanus* abundances from several locations in the North-East Atlantic. The results of this dissertation show that climate and temperature are the key factors causing variability in *Calanus* populations, but the mechanisms of *Calanus*-environment relationships vary among congeners and with location. The results also suggest that the variability of *Calanus* phenology and environmental effects on phenology can be studied with an alternative approach (vertical life table approach), that is based on abundance data-series limited to only one season each year. This dissertation broadens the understanding of zooplankton variability and facilitates more detailed predictions of zooplankton variability in ecosystem models of the North Atlantic.

NORD
University

ISBN: 978-82-93165-20-0
Trykk: Trykkeriet, Nord universitet
www.nord.no