



Interannual phenological variability in two North-East Atlantic populations of *Calanus finmarchicus*

Marina Espinasse^a, Claudia Halsband^b, Øystein Varpe^{b,c}, Astthor Gislason^d, Kristinn Gudmundsson^d, Stig Falk-Petersen^{b,e} and Ketil Eiane^a

^aFaculty of Biosciences and Aquaculture, Nord University, Bodø, Norway; ^bAkvaplan-niva, Fram Centre, Tromsø, Norway; ^cThe University Centre in Svalbard (UNIS), Longyearbyen, Norway; ^dMarine and Freshwater Research Institute, Reykjavik, Iceland; ^eNorwegian Polar Institute, Fram Centre, Tromsø, Norway

ABSTRACT

Phenological variations of the marine copepod *Calanus finmarchicus* were studied in Svalbard and northern Iceland, where samples were collected in summer and spring, respectively, over two decades. Four phenological indices, developed for copepodite stage-structured data, were used: the proportion of CV to total abundance (CVT), the population development index (PDI), the average weighted stage (AWS), and the average age in days (AAD). The variation of these indices was compared within and between locations to evaluate their suitability for the analysis of phenological effects. For both populations, phenology was related to local temperature and spring bloom dynamics, influenced by Atlantic water inflow. Large-scale climate was related to phenological variation only in the Svalbard population. *C. finmarchicus* phenology advanced under warmer conditions in both locations. We conclude that vertical phenological indices, i.e. based on interannual changes in copepodite stage structure, are useful to investigate zooplankton phenology, especially when data series covering the whole life cycle are unavailable. We suggest that AWS and AAD can be applied irrespective of sampling time, while PDI and CVT should be applied for early and late sampling seasons, respectively. When multiple phenological indices are needed, AAD in combination with either CVT or PDI should be preferred.

ARTICLE HISTORY

Received 12 January 2018
Accepted 24 July 2018
Published online 14 September 2018

SUBJECT EDITOR

Audrey Geffen

KEYWORDS

Calanus spp; phenology; vertical life table approach

Introduction

The timing of life cycle events and the timing of activities within the annual cycle of an organism (phenology) are important adaptations to the environment (McNamara and Houston 2008; Varpe et al. 2017). As phenological traits tend to be flexible and may readily change in response to environmental variability (Post 2013), studies of phenology may reveal species-environment relationships and provide new perspectives on how organisms respond to environmental fluctuations (Parmesan and Yohe 2003).

During the last decades, climate change caused warming of marine ecosystems in the North Atlantic (Walczowski et al. 2012) and the Arctic oceans (Wassmann et al. 2011). Climate change may result in large-scale regime shifts in marine ecosystems (Beaugrand et al. 2015). More commonly, however, climate variability is 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).

Many marine planktonic species are particularly sensitive to climate variability because ambient water temperature affects their physiological processes and alter the pelagic environment through the effects on thermal stratification and vertical mixing (Hays et al. 2005). The fitness of herbivorous plankton depends on the ability to time reproduction relative to the timing of the phytoplankton spring bloom (Varpe 2012), because temporal and spatial overlap between food-sensitive, early developmental stages of zooplankton and phytoplankton peaks results in increased survival (Cushing 1990). However, as climate change may alter timing and succession in plankton communities (Beaugrand et al. 2003; Edwards and Richardson 2004), the temporal overlap between the phytoplankton bloom and zooplankton may weaken and result in a mismatch between the phytoplankton bloom and food demand of zooplankton (Durant et al. 2007). Such mismatches may reduce food web productivity in high-latitude pelagic ecosystems, where the relatively short productive season leaves only a limited time window for growth (Leu et al. 2011).

The primarily herbivorous calanoid copepod *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 one of its core distribution areas in the Norwegian Sea, and its presence is associated with Atlantic waters throughout most of the North Atlantic area (Jaschnov 1970). *C. finmarchicus* usually has a one-year life cycle and reproduces in surface waters during or shortly after the spring phytoplankton bloom, from March to May (Marshall and Orr 1955; Melle and Skjoldal 1998).

The *C. finmarchicus* life cycle consists of six naupliar (NI to NVI) and six copepodite developmental stages, which include early copepodites (CI to CIII), late copepodites (CIV to CV), and adult males and females (CVI). Molting from one developmental stage to the next is often associated with important life cycle events such as the start of feeding (NIII), diapause (CV), and reproduction (CVI) (Marshall and Orr 1955; Hirche 1993).

Due to its ecological importance and sensitivity to climate variability, *C. finmarchicus* is often a target for phenological studies 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. Usually, the phenological changes in *Calanus* is assessed by various phenological proxies, or indices, based on abundance or population stage structure. Commonly used phenological indices include the sex ratio and the ratio of adults to CVs (Diel and Tande 1992), the timing of abundance peaks (Chiba et al. 2006; Mackas et al. 2012), the time when the population reaches cumulative abundance percentiles (Greve et al. 2005), the ratio of CVs to total abundance (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 more patterns of phenological variability and identifying more phenological responses to the environment (Thackeray et al. 2013).

Previous studies have reported that seasonal development of *Calanus* spp. can be influenced by climate change (Mackas et al. 2012). Under warmer climate in the North Atlantic, *C. finmarchicus* is expected to reproduce earlier and to complete more generations per year (Head et al. 2013), have a potentially shorter diapause duration (Wilson et al. 2016), and faster development (Kjellerup et al. 2012; Weydmann et al. 2018).

However, the phenological responses of *C. finmarchicus* appear to be non-uniform across the distribution area. *C. finmarchicus* stocks dwelling in different oceanographic domains tend to have unsynchronized phenological cycles, and therefore, are likely to be affected differently by fluctuations of sea temperature (Kvile et al. 2014). One reason for the difference in phenological responses is that changes in local hydrography, such as inflow of warm water masses, may accelerate developmental rate of *Calanus* and trigger a phenological shift (Kristiansen et al. 2016). On the other hand, local differences in phenology may reflect that populations at the margins of their distribution range have different sensitivity to environmental parameters, reflected in the effects on abundance and development, than populations near the core distribution area (Beaugrand et al. 2013). However, more knowledge is needed to understand how environmental variability is translated into phenological changes in *C. finmarchicus*.

Analysis of long-term *Calanus* data series has been successfully applied by earlier studies to describe abundance and distribution changes in *Calanus* populations (e.g. Beaugrand 2003; Gislason et al. 2014). In addition, long-term data on *Calanus* abundance or biomass have been used by modelling approaches to predict future changes in *Calanus* biogeography and occurrence under different environmental scenarios (Chust et al. 2014; Villarino et al. 2015). Similarly, previous research has demonstrated that long-term data series can be used to better understand and predict interannual changes in phenology (Edwards and Richardson 2004; Mackas et al. 2007). However, the analysis of long-term variability in phenology can be challenging due to low availability of data covering the whole life cycle of the species and thus, must largely rely on long-term but seasonally fragmented phenological data series.

This study applies long-term seasonal data series on *C. finmarchicus* in two locations in the North-East Atlantic (western Svalbard and northern Iceland) to quantify interannual variability in *C. finmarchicus* phenology using phenological indices based on the population stage structure. The aim of the study is to disentangle relationships between *C. finmarchicus* phenology and interannual environmental variability and to evaluate applicability of phenological indices that are based on seasonal population stage structure.

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 west coast of Svalbard and on the shelf off northern Iceland (Figure 1). Kongsfjorden (maximum depth- 400 m) is a glacial fjord, which is influenced by both Atlantic water masses through the West Spitsbergen Current (WSC; Figure 1), and by Arctic water masses from a coastal current (Svendsen et al. 2002). 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; Figure 1) as well as by Arctic water masses of the East Greenland Current (EGC) originating in the Arctic Ocean (Figure 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; Figure 1) in July 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 m² 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 overall depth bins and assuming 100% filtering efficiency of the net.

In northern Iceland, zooplankton was collected at 6 stations (Sig1–Sig17; ca 67°N, 18.5°W; Figure 1) by the

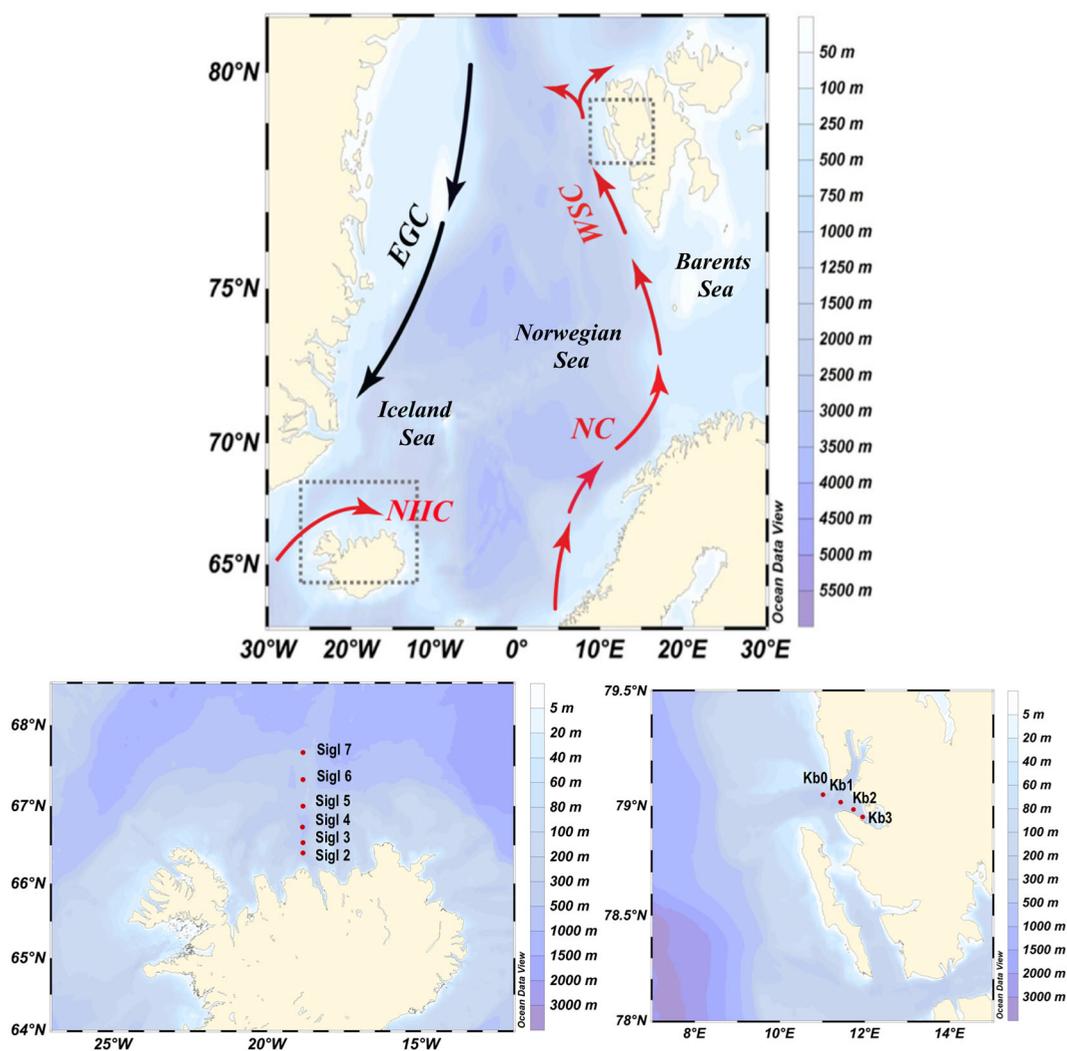


Figure 1. The current system in the northern North Atlantic (top panel) and sampling locations of *C. finmarchicus* data in Svalbard in July (bottom left) and in northern Iceland in May (bottom right). The sampling site in Svalbard is a transect of four stations (depth range 315–352 m), in northern Iceland – a transect of six stations (depth range 230–700 m). The codes for the oceanic currents are: NIIC – North Icelandic Irminger Current; NAC – Norwegian Atlantic Current; WSC – West Spitsbergen Current; EGC – East Greenland Current. Red and black arrows denote warm and cold water currents, respectively.

Marine and Freshwater Research Institute in Iceland in May every year from 1990 to 2011 (Sigl6 was not sampled in 2007). In 1990 and 1991, a Hensen plankton net (0.42 m² mouth area and 200 µm mesh size) was used, while all subsequent sampling was done with a WP2 plankton net (0.25 m² 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* tends to reside in the surface waters at sampling time (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 in the mouth of the net. We assumed that the two nets had the same characteristics with respect to sampling of *C. finmarchicus*.

All zooplankton samples were preserved in a 4% formaldehyde-in-seawater solution until enumeration in the lab. *Calanus* species separation in Svalbard and northern Iceland was based on prosome length distributions (Unstad and Tande 1991) and was done for randomly selected sub-samples as described in Daase et al. (2007) for Svalbard samples and in Gislason et al. (2009) for northern Iceland samples.

Molecular identification techniques suggest that *C. glacialis* in the North Atlantic can occasionally be misidentified as *C. finmarchicus*. The error rate can be at least 10% in Svalbard waters and along the Norwegian coast (Gabrielsen et al. 2012; Choquet et al. 2017), while precise estimations are not yet available for northern Iceland. Thus, in some samples analysed in this study, *C. finmarchicus* abundances can be overestimated, but it was not possible to quantify this error.

Environmental data

Salinity and temperature profiles were obtained by CTD casts (Sea-Bird Electronics) at each sampling station. In northern Iceland, also Chl *a* concentration was 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 yearly phytoplankton spring bloom, we used remote sensing data on Chl *a* concentration (available for 1998–2011) 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 × 4.63 km) were merged by a Garver, Sieleg and Maritorena (GSM) model (Maritorena et al. 2010). 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°) to avoid distortion by terrestrial inference. For northern Iceland, remote Chl *a* measurements were taken from a rectangular area (from 66°30'N to 67°45'N and from 17°30'W to 19°15'W), which enclosed all sampling stations. Chl *a* levels were extracted in R (R Core Team, 2016), using the package *ncdf4* (v.1.9; Pierce 2013). Missing Chl *a* values 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 the median Chl *a* concentration for that year and location by 5% (Henson et al. 2009).

As a proxy for large-scale environmental variability, we used annual values of the North Atlantic Oscillation index (NAO) and the Arctic Oscillation index (AO) (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.

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

Phenological indices and data analysis

So far, only a few data series from the sub-Arctic region cover the whole life cycle of *Calanus*. Limited data

Table 1. 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				
KB0	Multinet	315–200–100–50–20–0	July 1996–2010, Days 182–215	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

coverage complicates *Calanus* phenology studies, as most phenological indices rely on seasonal development of the populations. To overcome this problem, we applied alternative phenological indices that rely on stage-structured abundance data (copepodite stages only), collected over a short time period. Utilizing information on stage structure from 'snapshot data', with a limited coverage of the organism's life cycle, is referred to as a vertical life table approach (Aksnes and Ohman 1996; Aksnes et al. 1997). In this analysis, we applied four phenological indices developed in a vertical life table approach as follows.

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

$$CVT = \frac{N_{CV}}{N_{tot}}, \quad (1)$$

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),

$$PDI = \frac{N_{CI-CIII}}{N_{tot}}, \quad (2)$$

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

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

$$AWS = \frac{\sum_{k=1}^6 (w*k)}{\sum_{k=1}^6 w}, \quad (3)$$

where w is the proportion of each copepodite stage in the sample and k is the order of a copepodite stage (CI = 1, CII = 2, etc., adults = 6).

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

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

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

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

where T is ambient temperature in 0–50 m, and a and α are empirically fitted constants. The constant a is equal to 9.11 for all developmental stages, while constant α is

different for each developmental stage as estimated by Campbell et al. (2001).

CVT mainly reflects the variation of older copepodites in the population, while PDI is more sensitive to the variation in abundance of early copepodites. On the other hand, AWS depends on the variation of both early and older life stages, while AAD also takes the age of the population into account by assuming simple relationship between age and environmental variability (temperature). Therefore, the four phenological indices represent different stages and aspects of *Calanus* life cycle and when applied together, should provide a more complete overview of the species phenological variability (Thackeray et al. 2013). Using multiple phenological indices is especially relevant to our study, where *C. finmarchicus* from Svalbard and northern Iceland were sampled at different times of a year, and copepodite stage compositions were different between the locations.

The variability in the computed phenological indices deviated from normality, and indices contained outliers, hence a non-parametric statistical test was preferred throughout the data analysis. To test for trends in the phenological indices caused by variability in sampling time between years, we used a non-parametric correlation test (Kendall's correlation) and found that generally, the phenological indices were correlated with sampling time. Therefore, the phenological indices were de-trended with a moving average method (Legendre and Legendre 1998). First, we estimated the mean of each phenological index per day within the sampling window for all years pooled. Missing values of the mean phenological indices per day within the sampling window were modelled by imputation in the *mice* package in R (v. 2.25; Van Buuren and Groothuis-Oudshoorn 2011). Then, a 3-day moving average was calculated to smooth the daily means of phenological indices. The residuals were calculated by subtracting the moving average values from the daily means of the phenological indices. These residuals, representing a seasonal component of the data series (Turner et al. 2006), were then subtracted from the corresponding original values of the phenological indices per day of year within the sampling window to yield de-trended data series.

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 large-scale environmental variability (NAO, AO), Kendall's correlation test was applied. AAD was not correlated

against temperature, because this index is a function of temperature.

Results

Environmental variability

In Svalbard, salinity (0–50 m) increased ($\tau = 0.30$, $P = 0.002$), and in northern Iceland, both average temperature (0–50 m) and salinity increased over the study period ($\tau = 0.15$, $P = 0.014$ and $\tau = 0.13$, $P = 0.030$, respectively; Figure 2).

Average (0–50 m) temperature in Svalbard and northern Iceland was similar: 3.80°C (range = 1.90–5.30°C) and 3.58°C (range = 0.54–5.80°C), respectively (Figure 2). Salinity (0–50 m) was on average lower in Svalbard (33.62 psu, range = 30.00–34.40 psu) than in northern Iceland (34.75 psu, range = 34.30–35.00 psu; Figure 2).

The average date of the spring bloom start in Svalbard was day of year 150 (range = 130–168), and in northern Iceland, spring bloom started on average on day 154 (range = 127–173) (Figure 3). Average concentration of *in situ* Chl *a* in May in northern Iceland (the only location where it was measured) was 4.76 mg l⁻¹ (range = 0.31 to 12.0 mg l⁻¹) (Figure 3).

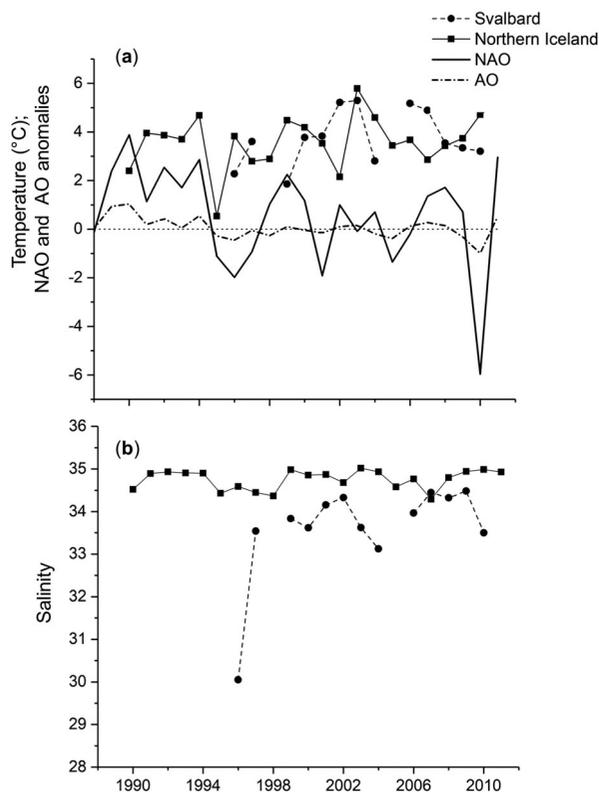


Figure 2. Average temperature (0–50 m, °C), NAO and AO annual indices (a) and salinity (b) over the sampling stations in Svalbard and northern Iceland.

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 $\tau = 0.32$, $P < 0.001$). The start date of the phytoplankton spring bloom in Svalbard correlated negatively with AO ($\tau = -0.41$, $P = 0.002$). In northern Iceland, only bloom timing correlated with AO ($\tau = 0.37$, $P < 0.001$).

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) (Figure 2). AO variability was synchronous with that of NAO, and the highest AO was observed in 1990 (1.02) and 2011 (0.52), while the lowest AO was observed in 2010 (-1.04).

C. finmarchicus abundance and stage structure

In the *C. finmarchicus* population in Svalbard in July, both early copepodites (CI–CIII) and late copepodites (CIV–CVI) were abundant in most years, except 2001, 2006, and 2007, when CIVs and CVs dominated in the population. In 2003 and 2004, all copepodite

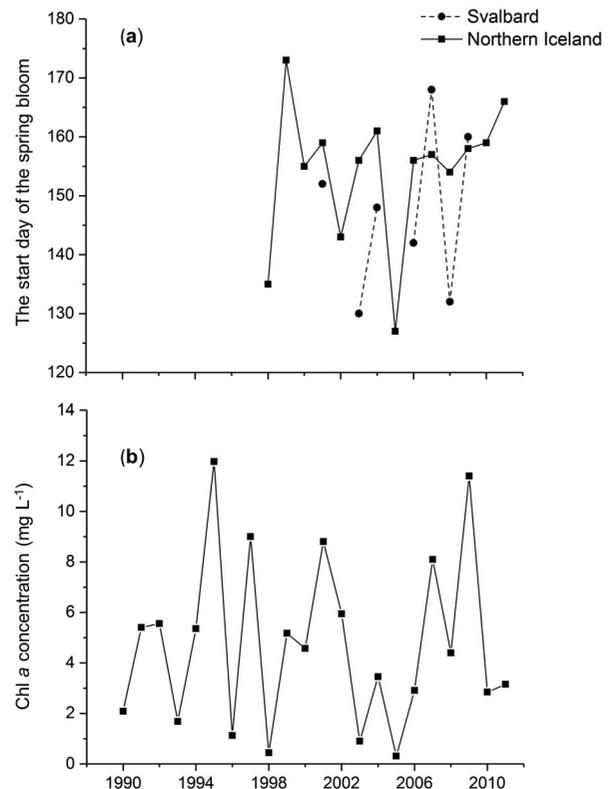


Figure 3. The average start day of the spring phytoplankton bloom in Svalbard and northern Iceland (a) and *in situ* Chl *a* concentration in northern Iceland (b). The spring bloom start was estimated from the remote sensors data on Chl *a* concentration. For the details of the calculation of the start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

abundances were relatively low in Svalbard – less than 17% of maximal observed abundance of copepodite stages (Figure 4).

In northern Iceland, early copepodites dominated in the population, and the highest abundance of early copepodites was observed in 2003 and 2005, but low (<5% of maximal observed abundance of copepodite stages) in the preceding years 2002 and 2004 (Figure 4). Older copepodite stages (CIVs to adults) occurred in low abundances (<13% of maximal abundance of copepodite stages observed) throughout the time series in northern Iceland (Figure 4).

Phenological indices

In Svalbard in July, CVT (the proportion of copepodites CV) ranged from 0.06 in 2009 to 0.48 in 2006 (Figure 5). CVT remained low between years 1996 and 2001 (around 0.12). CVT in northern Iceland in May was very low throughout the study period (range = 0.01–0.09).

PDI (the population development index) was generally lower in Svalbard in July (range 0.02–0.13) than in northern Iceland in May (range 0.27–0.93) (Figure 5). Interannual variability in PDI in Svalbard mirrored that of CVT. PDI peaked in 2009 (0.68), when the CVT was very low, and the lowest PDI (0.23) coincided with the highest CVT value in 2006. In northern Iceland, PDI was high in 1996, 1998, and 2002 (~ 0.93), but was very low in 1995 (0.26).

AWS (The average weighted stage) in Svalbard ranged from 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. AAD (the average age in days) 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) (Figure 5).

CVT and PDI correlated negatively in Svalbard, while CVT and AWS correlated positively (Table II). AAD did not correlate with other phenological indices in Svalbard (Table II). In northern Iceland, all phenological indices correlated (Table II). Correlations were positive between CVT and AWS, between CVT and AAD, and between AWS and AAD, while all indices correlated negatively with PDI.

Phenology and environmental variability

In Svalbard, CVT correlated positively with temperature and AO, while PDI correlated negatively with both temperature and AO (Table III). In northern Iceland, CVT correlated positively with the spring bloom start,

while PDI correlated negatively with the spring bloom start. AWS correlated positively with AO and temperature in Svalbard, and positively with the spring bloom start and Chl *a* concentration in northern Iceland. While AAD correlated negatively with AO and salinity in Svalbard, it was negatively related only to salinity in northern Iceland (Table III).

Discussion

While large-scale climate effects on phenology were observed in Svalbard only, our results indicate that local environmental variability (hydrography and the timing of the phytoplankton spring bloom) was an important driver of interannual phenological variability in *Calanus* in both study areas. This agrees with previous findings in the North Atlantic, which show that zooplankton phenology is mainly driven by local temperature (Mackas et al. 2012).

The relationship between *Calanus* phenology and ambient temperature in Svalbard (Table III) implied that during sampling in July the population contained more of the older copepodite stages in years when water temperature was relatively high (2002, 2006; Figure 2). In Kongsfjorden, high water temperature is usually observed in years with significant influxes of warm Atlantic waters from the West Spitsbergen Current (Cottier et al. 2005; Walczowski et al. 2012; Figure 1). Increased water temperature probably contributed to faster development of *C. finmarchicus* (Campbell et al. 2001), and thus, a larger fraction of the population had developed through early copepodite stages at sampling time (July) in relatively warm years, provided that reproduction occurred at approximately the same time each year. Faster development and thus, shorter stage durations (Corkett et al. 1986), resulted in a lower AAD, contributing to correlation between higher salinity, as an indicator of Atlantic water masses, and low AAD (Table III).

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), further contributing to high proportions of older copepodites of *C. finmarchicus* in years with large Atlantic inflow.

Although variability in water masses likely affected phytoplankton bloom dynamics, we did not observe correlations between the timing of the phytoplankton spring bloom and *Calanus* phenology in Svalbard. We speculate that the lack of correlation between phytoplankton bloom dynamics and *Calanus* phenology in

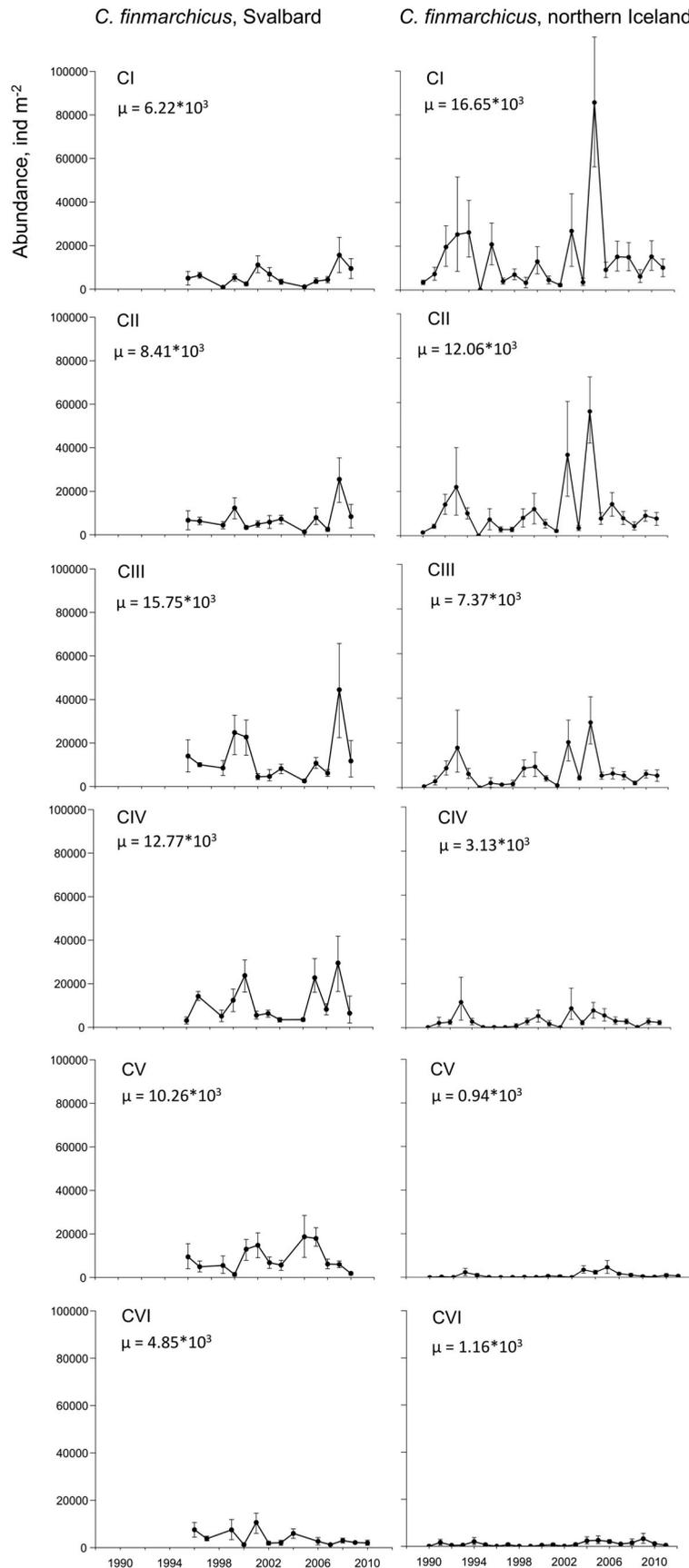


Figure 4. Average copepodite stage abundances from Svalbard in July (left), and in northern Iceland in May (right). CI, CII, CIII, CIV, CV denote copepodite stage abundances I through V, and CVI is the sum of adult male and female abundances. Error bars denote 95% bootstrapped confidence intervals.

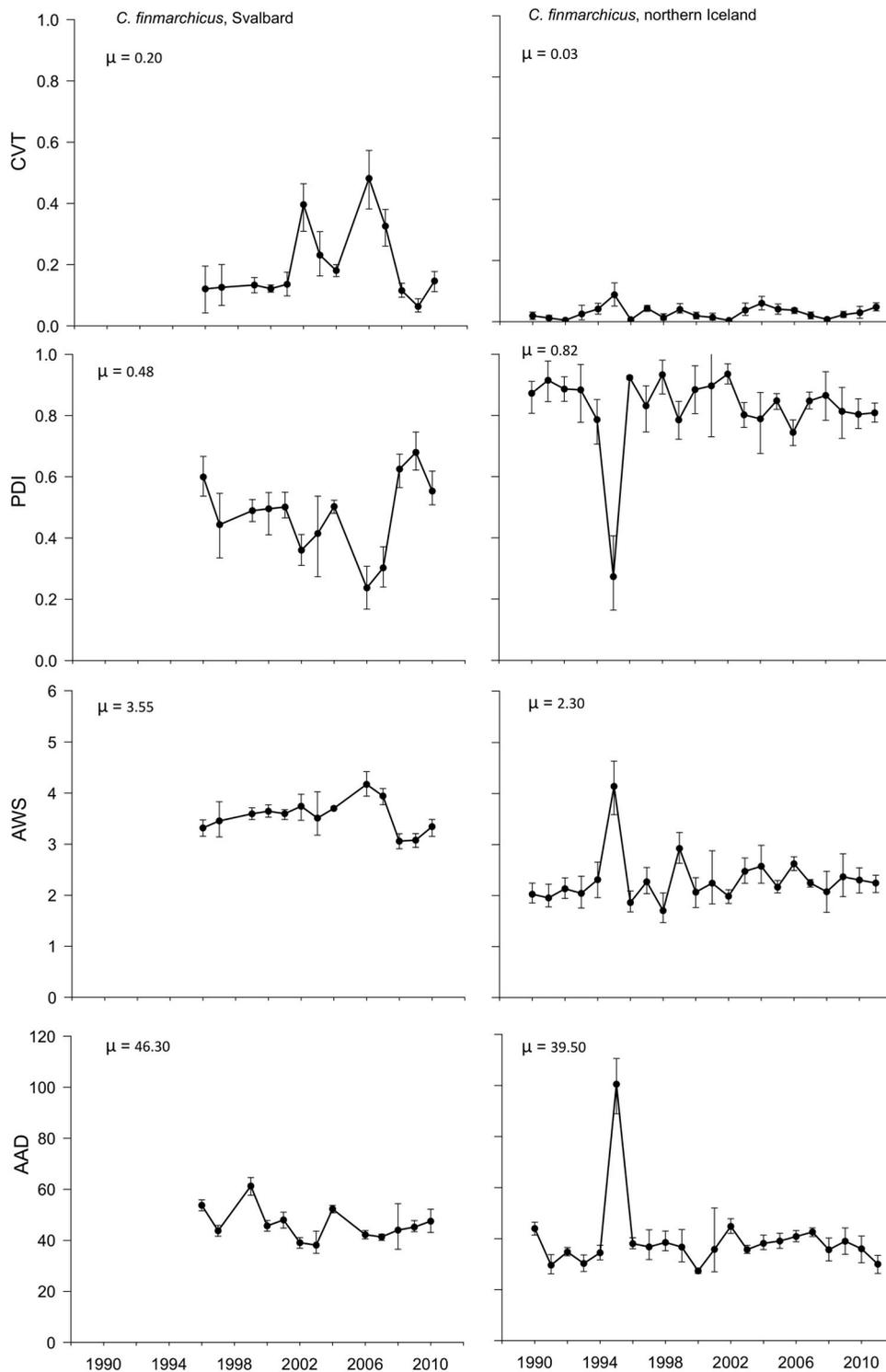


Figure 5. Yearly averages of de-trended phenological indices in Svalbard in July (left) and northern Iceland in May (right). Phenological indices are abbreviated as follows: CVT – the proportion of copepodites CV to total abundance; PDI – population development index or the proportion of copepodites CI through CIII to total abundance; AWS – average weighted stage; AAD – average age in days. Error bars denote 95% bootstrapped confidence intervals.

Svalbard can be attributed to relatively late sampling time in Svalbard (July), several months after the phytoplankton bloom and main spawning of *Calanus* (Melle and Skjoldal 1998). Therefore, the effect of spring

bloom on *Calanus* phenology may have been diluted compared to northern Iceland, where sampling was done earlier, in spring, and thus, closer to the occurrence of both *Calanus* reproduction and the spring bloom.

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.

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

Notes: Abbreviations for phenological indices are: CVT – proportion of copepodites CV to total abundance; PDI – population development index or the proportion of copepodites CI through CIII to total abundance; AWS – average weighted stage; AAD – average age in days.

We suggest that the relationship between AO and *C. finmarchicus* phenology in Svalbard reflected local climate and hydrography changes driven by AO variability. In the Arctic, high AO is associated with elevated temperatures (Kerr et al. 1999). Higher temperatures, in turn, accelerate *Calanus* growth and development, but this effect is probably complicated and difficult to discern, due to additional effect of Atlantic water inflow.

The correlation between CVT, AWS, PDI and the spring bloom start in northern Iceland, indicated that spawning of *C. finmarchicus* was timed with the onset of the spring bloom, as in the other locations in the

Table III. Statistically significant correlations between phenological indices of *C. finmarchicus* from Svalbard and northern Iceland and environmental parameters AO (Arctic Oscillation), T (temperature), S (salinity), Bloom (start date of the phytoplankton 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.

Location	Phenological index	Environmental variables	df	τ	P
Svalbard	CVT	AO	48	0.31	0.002
		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
	PDI	Bloom	81	-0.19	0.015
	AWS	Chl <i>a</i>	129	0.13	0.022
		Bloom	81	0.26	0.001
	AAD	S	129	-0.32	< 0.001

Notes: Abbreviations for phenological indices are: CVT – proportion of copepodites CV to total abundance; PDI – population development index or the proportion of copepodites CI through CIII to total abundance; AWS – average weighted stage; AAD – average age in days.

North Atlantic (Diel and Tande 1992; Durbin et al. 2000). Thus, in years with a later spring bloom start (e.g. 1999; Figure 3), the abundance of older stages in May was high relative to the abundance of early copepodites (CI to CIII).

The interaction between the inflows of Atlantic and Arctic water masses in northern Iceland is a key driver of the variability in *C. finmarchicus* abundance (Gislason 2005). Advection of warmer Atlantic waters from the south-west off Iceland transports some *C. finmarchicus* to northern Icelandic waters, but also promotes primary productivity and *C. finmarchicus* spawning (Asthorsson et al. 1983). Increased primary productivity, thereby may have further contributed to higher abundances of early *C. finmarchicus* copepodites during sampling in spring in years with high Atlantic waters inflow.

In contrast, years when Arctic water masses dominate in northern Icelandic 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). The early and relatively short phytoplankton bloom may result in a reduced *C. finmarchicus* spawning due to low food availability, as was also observed in the Norwegian Sea (Niehoff et al. 2000). In turn, reduced egg production results in lower recruitment of early life stages to the population and a delayed development from nauplii to early copepodites. Altogether, low recruitment and delayed development may explain relatively high abundances of overwintering stages and low total *C. finmarchicus* abundance observed in 1995 in northern Iceland. Similarly, negative correlation between AAD and salinity (Table III) indicated that in colder years, when the inflow of less saline, Arctic waters increased (Gudmundsson 1998), reproduction and recruitment of *C. finmarchicus* was reduced, and the population still largely consisted of the older, overwintered individuals in spring.

An optimal timing of seasonal events such as arousal from overwintering and the start of reproduction, can vary between *Calanus* individuals originating from different locations (Fiksen 2000; Varpe et al. 2012). Such life-history differences can be observed as phenological differences between *Calanus* originating from different water masses. In the southern Norwegian Sea, *C. finmarchicus* usually starts reproduction earlier in locations influenced mainly by Atlantic water masses than in locations influenced primarily by Arctic waters (Gaard and Nattestad 2002). The differences in *C. finmarchicus* phenology between the two oceanographic domains are in turn indicated by the population

stage structure: a higher proportion of early *C. finmarchicus* copepodites in spring is observed in locations with prevailing Atlantic water masses than in locations with a higher Arctic water masses inflow (Kristiansen et al. 2016). In our locations, the effect of water masses on phenology was analogous – a more advanced phenological development was observed when Atlantic water masses dominated in the study locations.

Temperature or its correlates – salinity or the dynamics of primary production in spring, appeared to be significant drivers of *C. finmarchicus* phenology in both locations (Table IV), supporting the notion that temperature plays a key role for inducing phenological variability in a range of marine and terrestrial animals (Sparks et al. 2000; Hays et al. 2005; Menzel et al. 2006). Temperature effects on plankton are often considered in studies of climate effects (Edwards and Richardson 2004; Feng et al. 2018), and the results of these studies suggest that plankton tend to follow an ‘earlier when warmer’ strategy (Mackas et al. 2012). A similar tendency was found in 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, earlier development was likely mediated by an earlier spawning of *C. finmarchicus* during warm years than during cold years.

Although climate drives phenology of many marine and terrestrial organisms (Parmesan and Yohe 2003; Körner and Basler 2010; Asch 2015), climate (as indexed by AO) was a correlate of *C. finmarchicus* phenology only in one of the two locations in this study. 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, *Calanus* variability is largely driven by the strength of Atlantic water inflow (Gislason et al. 2014), which is affected by the local wind regime rather than by direct effects of NAO or AO (Stefánsson and Gudmundsson 1969). In line with these findings, we did not observe direct correlation between *C. finmarchicus* phenology and climatic indices in northern Iceland in our data set. Similarly, the lack of correlation between *Calanus* phenology and NAO in Svalbard may be caused by the time lag between main NAO effects on hydrography in the North Atlantic (Visbeck et al. 2013) and responses of Arctic marine biota to such effects (Espinasse et al. 2017).

Comparison of the phenological indices

The CVT index is used in several studies to time the seasonal peak abundance of copepods (Mackas et al. 1998;

Mackas et al. 2007). In our study, we analysed data collected over a relatively short time each year and we could not identify seasonal abundance peak. Thus, we applied 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 year, they represented 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 (Figure 5), thus CVT in Svalbard is a suitable indicator of interannual phenological variability (Table IV). In northern Iceland, where data were collected close to the peak of *C. finmarchicus* spawning, CVT was small and showed limited variability between years. Thus, phenological shifts occurring during this season may not be detected by the CVT index. The PDI index, on the other hand, reflects the proportion of early copepodites. High relative abundance of early copepodites can be observed about a month after the main spawning event in *C. finmarchicus* (Campbell et al. 2001). PDI, thus, is a more suitable phenology index in the northern Iceland data set (Table IV), where *C. finmarchicus* population was largely consisted of early copepodite stages.

AWS seemed to be less dependent on the sampling season 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.

The variability in AAD reflected ambient temperature fluctuations in the study locations. In 1999 and 2004, low surface water temperatures in Svalbard (Figure 2) concurred with a peak in AAD, which implied that in cold years, the development from nauplii to older copepodite stages took relatively longer time. Similarly, in northern Iceland, the comparatively cold year 1995 coincided with a highest AAD (Figures 2 and 5).

In the coldest year in northern Iceland in our study (1995), both the lowest PDI and highest AWS and AAD occurred. However, in years with near-average temperature, the variability in AAD was not always synchronous with the variability in the other indices (Figure 5). The discrepancy in the synchronization between AAD and other phenological indices probably occurred because copepodite stage composition and duration of copepodite stages are non-linearly related to small changes in temperature. However,

Table IV. Suitable phenological indices and suggested environmental drivers of *C. finmarchicus* phenology in Svalbard and northern Iceland. Potential mechanisms linking environmental variability to *C. finmarchicus* phenology are indicated.

Location and month	Suitable vertical indices	Main drivers of phenology	Mechanisms of relationships
Svalbard, July	CVT, AAD	Temperature	The inflow of warm Atlantic water masses accelerates the development of <i>C. finmarchicus</i>
		AO	Warmer temperatures during high AO – faster development of copepodites
Northern Iceland, May	PDI, AAD	Hydrography and bloom dynamics	The inflow of Arctic waters decreases reproduction and development of early life stages. The inflow of warmer Atlantic waters has an opposite effect on <i>C. finmarchicus</i> phenology. Early and longer spring bloom positively affects timing and intensity of <i>C. finmarchicus</i> reproduction

Notes: Abbreviations for phenological indices are: CVT – proportion of copepodites CV to total abundance; PDI – population development index or the proportion of copepodites CI through CIII to total abundance; AWS – average weighted stage; AAD – average age in days.

the question of how population age and stage structure relate to temperature needs more investigation, as currently, the function describing the responses of the population age to temperature assumes constant ambient temperature during copepodite stages development (Corkett et al. 1986) and does not account for temperature changes due to water masses advection.

Because index AAD combines information on both population development (copepodite stage structure) and age (developmental time), it provides an alternative index, that can be useful in combination with more season-dependent and copepodite stage structure-based indices such as PDI or CVT. Thus, regardless of the season of sampling, at least two indices can be included in phenological studies where several phenological metrics are required (Table IV).

Concluding remarks

Similar to interannual variability in population abundances (Espinasse et al. 2017), phenological variability in *C. finmarchicus* reflected environmental variability, most notably, water temperature or spring bloom dynamics (Table IV). Large-scale climate effects, as indicated by AO variability, were important for *Calanus* phenology in the Svalbard population only, and likely affected *Calanus* populations indirectly, through the variability in hydrography, local climate, and primary production.

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

chosen according to the sampling period, and the second is AAD, because AAD is a less season-dependent index, directly reflecting temperature effects on phenology (Table IV).

Although not considered in this study, internal drivers such as the level of lipid accumulation, are additional factors that may influence *Calanus* phenology. Lipid reserves are essential for maturation of older copepodites (Hirche 1993), but may also be used to start reproduction earlier, before the main event of the spring phytoplankton bloom (Irigoinen 2004; Bandara et al. 2018). The amount of accumulated lipids before overwintering may have an indirect effect on the timing of reproduction, and in turn, on the recruitment of the next generation. Thus, future studies may be able to disentangle more of the phenological variability in *Calanus* if in addition to environmental factors they account for the amount of energetic reserves of *Calanus* copepodites prior to overwintering.

The role of predation on *Calanus* phenology could not be assessed in this work. The lack of predator data in our study 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), mismatch, or lack of temporal overlap, may develop between the seasonal peak of zooplankton and ecologically important planktivores, such as early stages of fish. Eventually, seasonal predation pressure on *Calanus* may also change. However, the responses of *Calanus* phenology to the variability 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 to provide a more comprehensive picture of *Calanus* seasonal variability.

Acknowledgements

We are thankful to M. Daase (UiT The Arctic University of Norway) 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.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by ConocoPhillips: [Grant Number NSBU-107021]; Lundin Norway [Grant Number C000353].

References

- Aksnes DL, Miller CB, Ohman MD, Wood SN. 1997. Estimation techniques used in studies of copepod population dynamics – a review of underlying assumptions. *Sarsia*. 82:279–96.
- Aksnes DL, Ohman MD. 1996. A vertical life table approach to zooplankton mortality estimation. *Limnology and Oceanography*. 41:1461–69.
- Asch RG. 2015. Climate change and decadal shifts in the phenology of larval fishes in the California current ecosystem. *Proceedings of the National Academy of Sciences*. 112:E4065–E4074. doi:10.1073/pnas.1421946112.
- Astthorsson O, Hallgrímsson I, Jónsson GS. 1983. Variations in zooplankton densities in Icelandic waters in spring during the years 1961–1982. *Rit Fiskideildar*. 7:73–113.
- Atkinson A, Harmer RA, Widdicombe CE, Mcevoy AJ, Smyth TJ, Cummings DG, Somerfield PJ, Maud JL, Mcconville K. 2015. Questioning the role of phenology shifts and trophic mismatching in a planktonic food web. *Progress in Oceanography*. 137:Part B:498–512. doi:10.1016/j.pocean.2015.04.023.
- Bandara K, Varpe Ø, Ji R, Eiane K. 2018. A high-resolution modeling study on diel and seasonal vertical migrations of high-latitude copepods. *Ecological Modelling*. 368:357–76. doi:10.1016/j.ecolmodel.2017.12.010.
- Beaugrand G, Brander KM, Lindley JA, Souissi S, Reid PC. 2003. Plankton effect on cod recruitment in the North Sea. *Nature*. 426:661–64. doi:10.1038/nature02164.
- Beaugrand G, Conversi A, Chiba S, Edwards M, Fonda-Umani S, Greene C, Mantua N, Otto SA, Reid PC, Stachura MM, et al. 2015. Synchronous marine pelagic regime shifts in the Northern Hemisphere. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 370 (1659):20130272. 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. *Progress in Oceanography*. 111:75–90. doi:10.1016/j.pocean.2012.11.002.
- Campbell RG, Wagner MM, Teegarden GJ, Boudreau CA, Durbin EG. 2001. Growth and development rates of the copepod *Calanus finmarchicus* reared in the laboratory. *Marine Ecology Progress Series*. 221:161–83. doi:10.3354/meps221161.
- 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 Biology*. 12:907–20. doi:10.1111/j.1365-2486.2006.01136.x.
- Chust G, Castellani C, Licandro P, Ibaibarriaga L, Sagarminaga Y, Irigoien X. 2014. Are *Calanus* spp. shifting poleward in the North Atlantic? A habitat modelling approach. *ICES Journal of Marine Science*. 71:241–53. doi:10.1093/icesjms/fst147.
- Choquet M, Hatlebakk M, Dhanasiri AK, Kosobokova K, Smolina I, Søreide JE, Svendsen C, Melle W, Kwaśniewski S, Eiane K. 2017. Genetics redraws pelagic biogeography of *Calanus*. *Biology Letters*. 13:20170588. doi:10.1098/rsbl.2017.0588.
- Cohen J, Barlow M. 2005. The NAO, the AO, and global warming: How closely related? *Journal of Climate*. 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.
- 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 CE, editor. *Proceedings of the second international conference on Copepoda* no 58. Ottawa: The National Museum of Ottawa; p. 539–46.
- Cottier FR, Nilsen F, Inall ME, Gerland S, Tverberg V, Svendsen H. 2007. Wintertime warming of an Arctic shelf in response to large-scale atmospheric circulation. *Geophysical Research Letters*. 34:L18504. doi:10.1029/2007GL029948.
- 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. *Journal of Geophysical Research*. 110:113. doi:10.1029/2004JC002757.
- Cushing DH. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. In: Blaxter JHS & Southward AJ, editors. *Advances in Marine Biology*. 26:249–93.
- 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. *Journal of Plankton Research*. 29:903–11. doi:10.1093/plankt/fbm068.
- Durant JLM, Hjermann DÅ, Ottersen G, Stenseth NC. 2007. Climate and the match or mismatch between predator requirements and resource availability. *Climate Research*. 33:271–83. doi:10.3354/cr033271.
- Diel S, Tande K. 1992. Does the spawning of *Calanus finmarchicus* in high latitudes follow a reproducible pattern? *Marine Biology*. 113:21–31. doi:10.1007/bf00367634.
- Durbin EG, Garrahan PR, Casas MC. 2000. Abundance and distribution of *Calanus finmarchicus* on the Georges Bank during 1995 and 1996. *ICES Journal of Marine Science*. 57:1664–85. doi:10.1006/jmsc.2000.0974.

- Edwards M, Richardson AJ. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature*. 430:881–84. doi:10.1038/nature02808.
- 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 Biology*. 40:2363–80. 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, editor. Arctic alpine ecosystems and people in a changing environment. Berlin: Springer; p. 147–66.
- Feng Z, Ji R, Ashjian C, Campbell R, Zhang J. 2018. Biogeographic responses of the copepod *Calanus glacialis* to a changing Arctic marine environment. *Global Change Biology*. 24(1):e159–e170. doi:10.1111/gcb.13890.
- Fiksen Ø. 2000. The adaptive timing of diapause – a search for evolutionarily robust strategies in *Calanus finmarchicus*. *ICES Journal of Marine Science*. 57:1825–33. doi:10.1006/jmsc.2000.0976.
- Gaard E, Nattestad K. 2002. Feeding, reproduction and seasonal development of *Calanus finmarchicus* in relation to water masses and phytoplankton in the southern Norwegian Sea. *ICES CM 2002/N:08*. 16 pages.
- Gabrielsen TM, Merkel B, Søreide JE, Johansson-Karlsson E, Bailey A, Vogedes D, Nygard H, Varpe Ø, Berge J. 2012. Potential misidentifications of two climate indicator species of the marine arctic ecosystem: *Calanus glacialis* and *C. finmarchicus*. *Polar Biology*. 35:1621–28. doi:10.1007/s00300-012-1202-7.
- Gislason A. 2005. Seasonal and spatial variability in egg production and biomass of *Calanus finmarchicus* around Iceland. *Marine Ecology Progress Series*. 286:177–92. doi:10.3354/meps286177.
- 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. *Journal of Plankton Research*. 31(5):541–51. doi:10.1093/plankt/fbp007.
- Gislason A, Silva T. 2012. Abundance, composition, and development of zooplankton in the Subarctic Iceland Sea in 2006, 2007, and 2008. *ICES Journal of Marine Science*. 69:1263–76. doi:10.1093/icesjms/fss070.
- 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 Journal of Marine Science*. 71:2539–49. doi:10.1093/icesjms/fsu098.
- Greene CH, Pershing AJ. 2007. OCEANS: climate drives sea change. *Science*. 315:1084–85. doi:10.1126/science.1136495.
- Greve W, Prinage S, Zidowitz H, Nast J, Reiners F. 2005. On the phenology of North Sea ichthyoplankton. *ICES Journal of Marine Science*. 62:1216–23. doi:10.1016/j.icesjms.2005.03.011.
- Gudmundsson K. 1998. Long-term variation in phytoplankton productivity during spring in Icelandic waters. *ICES Journal of Marine Science*. 55:635–43. doi:10.1006/jmsc.1998.0391.
- Hays GC, Richardson AJ, Robinson C. 2005. Climate change and marine plankton. *Trends in Ecology and Evolution*. 20:337–44. doi:10.1016/j.tree.2005.03.004.
- Head EJM, 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. *Progress in Oceanography*. 114:46–63. doi:10.1016/j.pocean.2013.05.004.
- Henson SA, Dunne JP, Sarmiento JL. 2009. Decadal variability in North Atlantic phytoplankton blooms. *Journal of Geophysical Research*. 114:753. doi:10.1029/2008JC005139.
- Hirche HJ, Kattner G. 1993. Egg production and lipid content of *Calanus glacialis* in spring: indication of a food-dependent and food-independent reproductive mode. *Marine Biology*. 117:615–22. doi:10.1007/BF00349773.
- Hollowed AB, Sundby S. 2014. Change is coming to the northern oceans. *Science*. 344:1084–85. doi:10.1126/science.12511166.
- Irigoin X. 2004. Some ideas about the role of lipids in the life cycle of *Calanus finmarchicus*. *Journal of Plankton Research*. 26:259–63. doi:10.1093/plankt/fbh030.
- Jaschnov WA. 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.
- Kendall MG. 1970. Rank correlation methods. London: Griffin. 160 pages.
- Kerr RA. 1999. A new force in high-latitude climate. *Science*. 284:241–42. doi:10.1126/science.284.5412.241.
- Kjellerup S, Dünweber M, Swailethorp R, Nielsen T, Møller EF, Markager S, Hansen BW. 2012. Effects of a future warmer ocean on the coexisting copepods *Calanus finmarchicus* and *C. glacialis* in Disko Bay, western Greenland. *Marine Ecology Progress Series*. 447:87–108. doi:10.3354/meps09551.
- Körner C, Basler D. 2010. Phenology under global warming. *Science*. 327:1461–62. doi:10.1126/science.1186473.
- Kristiansen I, Gaard E, Hátún H, Jónasdóttir S, Ferreira ASA. 2016. Persistent shift of *Calanus* spp. in the southwestern Norwegian Sea since 2003, linked to ocean climate. *ICES Journal of Marine Science*. 73(5):1319–29. doi:10.1093/icesjms/fsv222.
- Kvile KØ, Dalpadado P, Orlova E, Stenseth NC, Stige LC. 2014. Temperature effects on *Calanus finmarchicus* vary in space, time and between developmental stages. *Marine Ecology Progress Series*. 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. *Journal of Plankton Research*. 25:1–20. doi:10.1093/plankt/25.1.1.
- Legendre P, Legendre LF. 1998. Numerical ecology. Amsterdam: Elsevier. 989 pages.
- Leu E, Søreide JE, Hessen DO, 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. *Progress in Oceanography*. 90:18–32. doi:10.1016/j.pocean.2011.02.004.
- Mackas DL, Batten S, Trudel M. 2007. Effects on zooplankton of a warmer ocean: recent evidence from the Northeast

- Pacific. *Progress in Oceanography*. 75:223–52. doi:10.1016/j.pocean.2007.08.010.
- Mackas DL, Goldblatt R, Lewis AG. 1998. Interdecadal variation in developmental timing of *Neocalanus plumchrus* populations at Ocean Station P in the subarctic North Pacific. *Canadian Journal of Fisheries and Aquatic Sciences*. 55:1878–93 doi:10.1139/f98-080.
- Mackas DL, Greve W, Edwards M, Chiba S, Tadokoro K, Eloire D, Mazzocchi MG, Batten S, Richardson AJ, Johnson C, et al. 2012. Changing zooplankton seasonality in a changing ocean: comparing time series of zooplankton phenology. *Progress in Oceanography*. 97–100:31–62. doi:10.1016/j.pocean.2011.11.005.
- Maps F, Runge JA, Leising A, Pershing AJ, Record NR, Plourde S, Pierson JJ. 2012. Modelling the timing and duration of dormancy in populations of *Calanus finmarchicus* from the Northwest Atlantic shelf. *Journal of Plankton Research*. 34:36–54. doi:10.1093/plankt/fbr088.
- 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 Sensing of Environment*. 114:1791–1804. doi:10.1016/j.rse.2010.04.002.
- Marshall SM, Orr AP. 1955. The biology of a marine copepod, *Calanus finmarchicus* Gunnerus. Edinburgh: Oliver & Boyd. 196 pages.
- Mcnamara JM, Houston AI. 2008. Optimal annual routines: behaviour in the context of physiology and ecology. *Philosophical Transactions: Biological Sciences*. 363:301–19. doi:10.2307/20208431.
- Melle W, Skjoldal HR. 1998. Reproduction and development of *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* in the Barents Sea. *Marine Ecology Progress Series*. 169:211–28. doi:10.3354/meps169211.
- Menzel A, Sparks TH, Estrella N, Koch E, Aasa A, Ahas R, Alm-Kübler K, Bissolli P, Braslavská OG, Briede A, et al. 2006. European phenological response to climate change matches the warming pattern. *Global Change Biology*. 12:1969–76. doi:10.1111/j.1365-2486.2006.01193.x.
- Niehoff B, Hirche HJ, Båmstedt U. 2000. The reproduction of *Calanus finmarchicus* in the Norwegian Sea in spring. *Sarsia*. 85:15–22. doi:10.1080/00364827.2000.10414552.
- Parmesan C, Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature*. 421:37–42. doi:10.1038/nature01286.
- Pierce D. 2013. ncd4: Interface to Unidata netCDF (Version 4 or Earlier) Format Data Files. R. package version 1.9. <https://CRAN.R-project.org/package=ncdf4>.
- Post E. 2013. Life history variation and phenology. In: Post E, editor. *Ecology of climate change – the importance of biotic interactions*. Oxford: Princeton University Press; p. 54–96.
- R Core Team. 2016. R: A language and environment for statistical computing. Vienna: R foundation for Statistical Computing.
- Sparks TH, Jeffree EP, Jeffree CE. 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.
- Stefánsson U, Gudmundsson G. 1969. Hydrographic conditions off the northeast coast of Iceland in relation to meteorological factors. *Tellus*. 21:245–58.
- Svendsen H, Beszczynska-Møller A, Hagen JO, Lefauconnier B, Tverberg V, Gerland S, Ørbæk JB, Bischof K, Papucci C, Zajaczkowski M, et al. 2002. The physical environment of Kongsfjorden–Krossfjorden, an Arctic fjord system in Svalbard. *Polar Research*. 21:133–66. doi:10.1111/j.1751-8369.2002.tb00072.x.
- Thackeray SJ, Henrys PA, Feuchtmayr H, Jones ID, Maberly SC, Winfield IJ. 2013. Food web de-synchronization in England's largest lake: an assessment based on multiple phenological metrics. *Global Change Biology*. 19:3568–80. doi:10.1111/gcb.12326.
- Thórdardóttir T. 1984. Primary production north of Iceland in relation to water masses in May–June 1970–1980. *ICES CM 1984/L*. 20:17.
- 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. *Marine Ecology Progress Series*. 311:115–24. doi:10.3354/meps311115.
- UNESCO/SCOR. 1996. Determination of photosynthetic pigments in seawater. Monographs in oceanographic methodology, vol. 1. Paris: UNESCO/SCOR. 69 pages.
- Unstad KH, Tande KS. 1991. Depth distribution of *Calanus finmarchicus* and *C. glacialis* in relation to environmental conditions in the Barents Sea. *Polar Research*. 10:409–20. doi:10.1111/j.1751-8369.1991.tb00662.x.
- Van Buuren D, Groothuis-Oudshoorn K. 2011. mice: Multivariate Imputation by Chained Equations in R. *Journal of Statistical Software*. 45(3):1–67. <http://www.jstatsoft.org/v45/i03/>.
- Varpe Ø. 2017. Life history adaptations to seasonality. *Integrative and Comparative Biology*. 57:943–60. doi:10.1093/icb/ix123.
- Varpe Ø. 2012. Fitness and phenology: annual routines and zooplankton adaptations to seasonal cycles. *Journal of Plankton Research*. 34:267–76. doi:10.1093/plankt/fbr108.
- 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*. 116:1331–42. doi:10.1111/j.0030-1299.2007.15893.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. *Marine Ecology Progress Series*. 531:121–142. doi:10.3354/meps11299.
- Visbeck M, Chassignet EP, Curry RG, Delworth TL, Dickson RR, Krahnemann G. 2013. The ocean's response to North Atlantic oscillation variability. In: Hurrell JW, Kushnir Y, Ottersen G, Visbeck M, editors. *The North Atlantic oscillation: climatic significance and environmental impact*. <https://agupubs.onlinelibrary.wiley.com/series/5064> Geophysical Monograph Series. Washington, DC: American Geophysical Union, p. 113–45.
- Walczowski W, Piechura J, Goszczko I, Wiczorek P. 2012. Changes in Atlantic water properties: an important factor in the European Arctic marine climate. *ICES Journal of Marine Science*. 69:864–69. doi:10.1093/icesjms/fss068.

- Wassmann P, Duarte CM, Agustí S, Sejr MK. 2011. Footprints of climate change in the Arctic marine ecosystem. *Global Change Biology*. 17:1235–49. doi:10.1111/j.1365-2486.2010.02311.x.
- Weydmann A, Walczowski W, Carstensen J, Kwaśniewski S. 2018. Warming of subarctic waters accelerates development of a key marine zooplankton *Calanus finmarchicus*. *Global Change Biology*. 24:172–83. doi:10.1111/gcb.13864.
- Wilson RJ, Banas NS, Heath MR, Speirs DC. 2016. Projected impacts of 21st century climate change on diapause in *Calanus finmarchicus*. *Global Change Biology*. 22(10): 3332–40. doi:10.1111/gcb.13282.