



## Contribution to the Symposium: 'Ecosystem Studies of Subarctic and Arctic Seas' Original Article

# Contribution of *Calanus* species to the mesozooplankton biomass in the Barents Sea

Johanna Myrseth Aarflot\*, Hein Rune Skjoldal, Padmini Dalpadado, and Mette Skern-Mauritzen

Institute of Marine Research (IMR), Bergen, PO Box 1870 Nordnes, N-5817, Norway

\*Corresponding author: tel: +47 41 104 205; fax: +47 55 238 531; e-mail: [johanna.aarflot@imr.no](mailto:johanna.aarflot@imr.no).

Aarflot, J. M., Skjoldal, H. R., Dalpadado, P., and Skern-Mauritzen, M. Contribution of *Calanus* species to the mesozooplankton biomass in the Barents Sea. – ICES Journal of Marine Science, 75: 2342–2354.

Received 7 September 2017; revised 15 November 2017; accepted 16 November 2017; advance access publication 15 December 2017.

Copepods from the genus *Calanus* are crucial prey for fish, seabirds and mammals in the Nordic and Barents Sea ecosystems. The objective of this study is to determine the contribution of *Calanus* species to the mesozooplankton biomass in the Barents Sea. We analyse an extensive dataset of *Calanus finmarchicus*, *Calanus glacialis*, and *Calanus hyperboreus*, collected at various research surveys over a 30-year period. Our results show that the *Calanus* species are a main driver of variation in the mesozooplankton biomass in the Barents Sea, and constitutes around 80% of the total. The proportion of *Calanus* decreases at low zooplankton biomass, possibly due to a combination of advective processes (low *C. finmarchicus* in winter) and size selective foraging. Though the *Calanus* species co-occur in most regions, *C. glacialis* dominates in the Arctic water masses, while *C. finmarchicus* dominates in Atlantic waters. The larger *C. hyperboreus* has considerably lower biomass in the Barents Sea than the other *Calanus* species. Stages CIV and CV have the largest contribution to *Calanus* species biomass, whereas stages CI–CIII have an overall low impact on the biomass. In the western area of the Barents Sea, we observe indications of an ongoing borealization of the zooplankton community, with a decreasing proportion of the Arctic *C. glacialis* over the past 20 years. Atlantic *C. finmarchicus* have increased during the same period.

**Keywords:** *C. finmarchicus*, *C. glacialis*, Fugløya-Bear Island transect, key drivers, mesozooplankton, temperature effects.

## Introduction

Herbivorous zooplankton plays an important role in the marine pelagic food web converting energy from primary production to food for higher trophic levels in the ecosystem. Copepods of the genus *Calanus* are predominantly herbivores and the most important zooplankton in the Nordic and Barents Sea ecosystems, largely due to their high abundances and lipid contents (Jaschnov, 1970; Tande, 1991; Melle and Skjoldal, 1998; Søreide *et al.*, 2008; Falk-Petersen *et al.*, 2009). Being a high latitude ecosystem, the Barents Sea is characterized by strong seasonality in light and sea-ice conditions, with large impact on the marine biota. Three

*Calanus* species are common here; *Calanus finmarchicus* is an Atlantic boreal species, while *Calanus glacialis* and *Calanus hyperboreus* are of Arctic origin (Conover, 1988; Tande, 1991; Melle and Skjoldal, 1998). Calanoid copepods are particularly well adapted to fluctuating environmental conditions due to reduced metabolic activity (diapause-like state) in winter when food is low, and capabilities of building large lipid reserves during the growing season. The individual lipid content in these species may be as large as 50–70% of the body weight (Lee, 1975; Scott *et al.*, 2000), which make them valuable food sources for higher trophic levels in the system. Indeed, the calanoid copepods constitute a key part of the

diet for many ecologically and economically important fish species in the Barents Sea (Wassmann *et al.* 2006; Orlova *et al.*, 2011; Dalpadado and Mowbray, 2013).

*Calanus finmarchicus* overwinters in deep waters (>500 m) of the Norwegian Sea, and is advected into the Barents Sea with the Atlantic current when it ascends to surface layers in spring (Skjoldal *et al.*, 1992; Torgersen and Huse, 2005). Advection from the Norwegian Sea is vital for sustaining the population in the Barents Sea (Torgersen and Huse, 2005; Skaret *et al.*, 2014), though local reproduction within the Barents Sea is also important (Kvile *et al.*, 2017). This species generally has a predominantly 1-year life cycle in these waters, with the new generation produced at the onset of the phytoplankton spring bloom (Tande *et al.*, 1985; Melle and Skjoldal, 1998). *Calanus glacialis* is a shelf species largely associated with Arctic water masses in the Barents Sea, and can have both 1- and 2-year life-cycles (Conover 1988; Tande, 1991; Melle and Skjoldal, 1998). The larger congener *C. hyperboreus* has in general low abundances in the Barents Sea (Hirche and Mumm, 1992; Melle and Skjoldal, 1998; Arashkevich *et al.*, 2002), with its centre of origin in the deep basins of the Greenland Sea and Baffin Bay where it can have up to a 4-year life cycle (Conover, 1988; Hirche, 1997).

Since around 1980, the Barents Sea has experienced a warming trend which has been particularly pronounced during the last two decades (Boitsov *et al.*, 2012; Smedsrud *et al.*, 2013). Warming has led to a northward shift in the spatial distribution of fish communities (Fossheim *et al.*, 2015) and to a marked increase in the amount of krill and cumulative biomass of pelagic species (Eriksen *et al.*, 2016, 2017b). Continued warming has increased the dominance of Atlantic species and negatively impacted the Arctic communities (Hirche and Kosobokova, 2007; Kjellerup *et al.*, 2012; Dalpadado *et al.*, 2014; Fossheim *et al.*, 2015; Frainer *et al.*, 2017). Short-lived species like plankton are expected to show rapid responses to a changing climate (Hays *et al.*, 2005), and changes at the base of the marine food chain may propagate through the system with consequences at an ecosystem scale (Beaugrand *et al.*, 2003; Helaouët and Beaugrand, 2007). Revealing ongoing changes in marine plankton (e.g. Beaugrand *et al.*, 2002) is therefore vital for predicting the future of marine ecosystems in a warmer climate.

The Barents Sea zooplankton community has been studied extensively (e.g. Hassel, 1986; Tande, 1991; Unstad and Tande, 1991; Melle and Skjoldal, 1998; Arashkevich *et al.*, 2002). Many studies point to the importance of the *Calanus* species due to their size, abundance and lipid contents, though few have quantified their contribution to the total mesozooplankton biomass. Furthermore, most studies have analysed samples from a restricted time-period of one or a few years with low seasonal resolution. We explored an extensive dataset of species abundance for *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus*, originating from various research and monitoring surveys in the Barents Sea, conducted by the Institute of Marine Research (IMR), Norway, over a 30-year period. IMR has used a standard method of splitting each zooplankton sample in two halves: one for determination of dry weight (dw) biomass, and the other preserved for species counts (Melle *et al.*, 2004). Our aim was to quantify the relationship between sampled mesozooplankton biomass and estimated biomass of *Calanus* species in the Barents Sea using the pair-wise samples. We further investigated the spatial patterns of the three species in relation to water masses and bottom topography, and evaluated whether there has been a change in the

copepod community concurrent with the recent warming in the area. A transition towards dominance of smaller-sized, Atlantic copepods could affect the lipid structure and energy flow in the ecosystem with consequences for many trophic levels in the food web.

## Material and methods

### Zooplankton sampling and analyses

The standard procedure for zooplankton sampling at the IMR, Norway, is described in detail in Melle *et al.* (2004) and Skjoldal *et al.* (2013). Briefly, samples are divided in two halves with a Motoda plankton splitter, one part for determining the biomass (g dw per m<sup>2</sup> or m<sup>3</sup>), and the other half for species identification and abundance estimation. The biomass subsample is separated into three size fractions using mesh gauzes of 2000, 1000, and 180 µm (for details, see Skjoldal *et al.*, 2013). The second subsample is preserved with buffered 4% formalin solution and stored for later processing. The three *Calanus* species are identified based on size limits (Supplementary Table S1) and morphological characteristics including shape of the curvature of the coxopodite of the fifth leg (P5) (Knutsen and Dalpadado, 2009), and counted separately for each copepodite stage (CI–CV and CVI females and males). Consistent size-limits have been used throughout the period of the samples used in our study (see Hassel, 1986; Melle and Skjoldal, 1998). The size frequency data typically follow normal distributions for each of the species, with some (and variable) overlap between them, particularly for *C. finmarchicus* and *C. glacialis* (Hassel, 1986; Unstad and Tande, 1991; Melle and Skjoldal, 1998; Parent *et al.*, 2011; Gabrielsen *et al.*, 2012). Use of fixed size limits to separate the species is therefore an approximation, and the potential for misidentifications is present, particularly in areas where the species co-occur. Individuals of intermediate size are therefore routinely examined for curvature of the coxopodite to reduce the degree of misidentification from the use of fixed size limits.

### Data description

Sample processing for species identification is labour-intensive, and only a fraction of the samples collected by the IMR are processed (all samples are stored in a long-term repository). Over the years, there has still been an accumulation of processed samples originating from various researches and monitoring surveys. We extracted all samples in the IMR database with data on both mesozooplankton biomass and species abundance from the same sampling stations in the Barents Sea (Tables 1 and 2). When multiple samples had been taken at a station, only one (WP2 gear, bottom to surface haul) was included in this study. In total, we analysed 616 samples covering an extensive geographical area (Figure 1). Samples were grouped into five oceanographic regions based on bathymetry and advection (Table 2), and aggregated into the following seasons: winter (November–March), spring (April–May), summer (June–July), and autumn (August–October). The Fugløya-Bear Island transect (FB transect, grey line in Figure 1) is a standard oceanographic transect in the western region, hereafter called “West”, covered by IMR five to eight times each year. Samples from this transect are regularly processed for species identification, and have consistent seasonal coverage since 1995. Region West therefore contributed a large part (~70%) to the data analysed in this study. Samples from the 1980s (the Pro Mare

**Table 1.** Gear characteristics of the sampling equipment in the dataset.

Sampling gear	Net opening (cm)	Mesh size ( $\mu\text{m}$ )	Lower sampling depth (m)	Sample unit	Samples (n)
WP2	56	180	100, bottom	$\text{m}^{-2}$	569
Juday	80	250, 375	40, 50	$\text{m}^{-2}$	14
Hufsa	–	180, 375	30, 40, 50, 100	$\text{m}^{-3}$	28
MOCNESS	100	180, 333	bottom	$\text{m}^{-3}$	5

For detailed gear descriptions, see Sameoto *et al.* (2000), Wiebe and Benfield (2003), and Skjoldal *et al.* (2013). Upper sampling depth for all gears is surface (0 m).

**Table 2.** Overview of regions as defined in this study, and number of samples analysed per region.

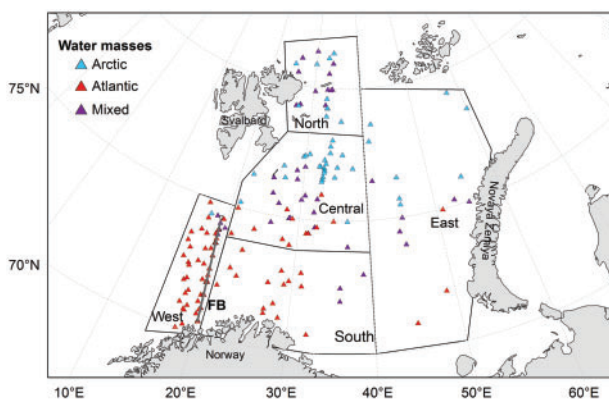
Region	Latitude ( $^{\circ}\text{N}$ )	Longitude ( $^{\circ}\text{E}$ )	Bottom depth (m) <sup>a</sup>	Dominating water mass <sup>b</sup>	Main sampling period <sup>c</sup>	Samples (n) per season	
West	70–75	15.5–21	266	Atlantic	1994–2016	Summer	65
						Autumn	170
						Winter	177
						Spring	89
South	70–73.5	21–40	317	Atlantic	1983–2016	Summer	9
						Autumn	7
						Winter	0
						Spring	3
Central	74–78	21–38	221	Arctic/mixed	1983–2009	Summer	33
						Autumn	15
						Winter	2
						Spring	6
North	78–82	25–36	211	Arctic/mixed	2005–2016	Summer	1
						Autumn	22
						Winter	0
						Spring	0
East	71–80	41–61	234	Arctic/mixed	1983–1994	Summer	5
						Autumn	11
						Winter	1
						Spring	0

Samples were aggregated into the seasons winter (November–March), spring (April–May), summer (June–July), and autumn (August–October).

<sup>a</sup>Mean of sampling stations.

<sup>b</sup>Dominating water mass in samples analysed: Atlantic ( $T > 3^{\circ}\text{C}$ ), Arctic ( $T < 0^{\circ}\text{C}$ ), mixed ( $0^{\circ}\text{C} < T < 3^{\circ}\text{C}$ ) based on temperature at 50-m depth.

<sup>c</sup>>90 % of samples taken during this period.



**Figure 1.** Geographical distribution of samples analysed in this study ( $n = 616$ ). The Barents Sea was divided into five oceanographic regions as defined in Table 2. Outer bounds of the polygons are included as a visual aid. Samples were defined as Arctic ( $T < 0^{\circ}\text{C}$ ), Atlantic ( $T > 3^{\circ}\text{C}$ ), or mixed ( $0^{\circ}\text{C} < T < 3^{\circ}\text{C}$ ) based on temperature data from 50 m depth. The FB transect, where a large part of the data originates from, is marked with a line.

programme; Sakshaug *et al.*, 2009) were mainly from the spring and summer period.

Most of the samples were from near-bottom to surface hauls, though  $\sim 10\%$  had shallower sampling depths (Table 1). Samples with a unit of abundance or biomass  $\text{m}^{-3}$  were converted to  $\text{m}^{-2}$  by integrating over the water column down to the lowest sampling depth. Differences in sampling gear and depth were accounted for in the statistical analyses.

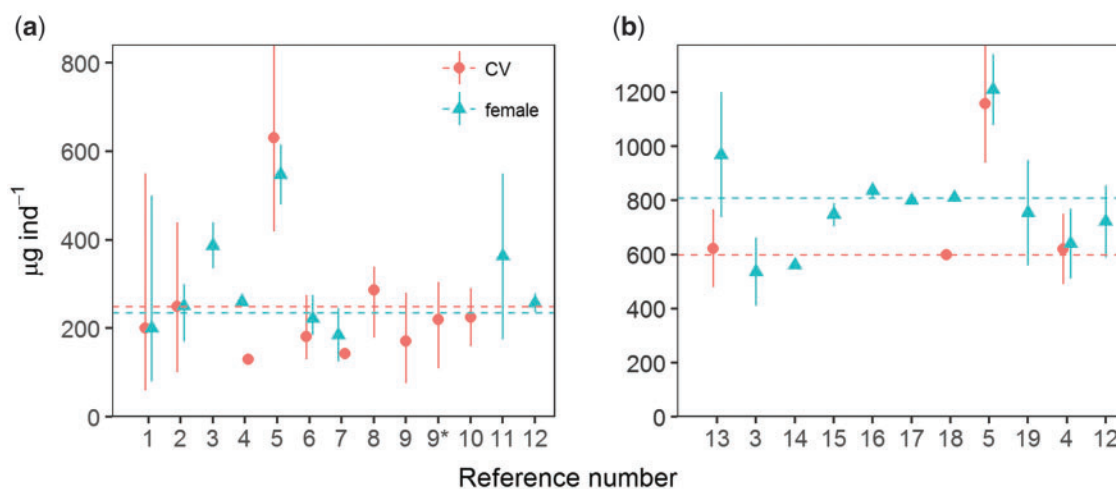
### Biomass estimation of *Calanus* species

Copepodite abundances of *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus* were converted to biomass estimates using individual weight-at-stage data from the literature (Table 3). The individual weight can vary considerably, by up to an order of magnitude within a copepodite stage (Figure 2). Part of this variation is due to weight increase as individuals grow through a stage between successive moults. There is also systematic variation in relation to thermal habitat, where individuals tend to become larger when they grow at low compared with higher temperature (Campbell *et al.*, 2001; Melle *et al.*, 2014). Mean weights from studies in or near the Barents Sea were considered representative of those for our study region (Table 3). We also performed length measurements on individuals of *C. finmarchicus* and

**Table 3.** Dry weight ( $\mu\text{g}$ ) per copepodite stage (CI–CVI female and male) for *Calanus* spp. used to estimate biomass in this study.

Species	CI	CII	CIII	CIV	CV	CVIf	CVIm	References
<i>C. finmarchicus</i>	1.5	4	13	70	250	235	235	Tande (1982), Tande and Slagstad (1992)
<i>C. glacialis</i>	8	16	40	185	600	810	600	Hanssen (1997), Hirche and Kosobokova (2003)
<i>C. hyperboreus</i>	10	40	140	500	2000	3500	3500	Hirche (1997)

See also Figure 2 for an overview of dry weight measurements of *C. finmarchicus* and *C. glacialis* from the literature.



**Figure 2.** Mean weight ( $\mu\text{g ind}^{-1}$ , points in figure) for copepodite stage CV and adult females of (a) *C. finmarchicus*, and (b) *C. glacialis*, as reported by the scientific literature (x-axis). (i) Carloti *et al.* (1993), (ii) Tande (1982), (iii) Ikeda and Skjoldal (1989), (iv) Scott *et al.* (2000), (v) Diel (1991), (vi) Hirche *et al.* (2001), (vii) Gislason (2005), (viii) Båmstedt and Ervik (1984), (ix) Jónasdóttir (1999) (\*deep water), (x) Heath and Jónasdóttir (1999), (xi) Runge *et al.* (2006), (xii) Kjellerup *et al.* (2012), (xiii) Båmstedt and Tande (1985), (xiv) Hirche (1987), (xv) Hirche and Kattner (1993), (xvi) Hirche *et al.* (1994), (xvii) Hirche and Kwasniewski (1997), (xviii) Hirche and Kosobokova (2003), (xix) Tourangeau and Runge (1991). Vertical lines show the range of weights, or mean  $\pm$  SD, when this information has been available. Horizontal lines show the values employed in this study when estimating species biomass for stage CV (dotted) and females (dashed).

*C. glacialis* stages CIV, CV and adult females, to evaluate the propriety of the weight-data employed for estimating species biomass. Based on these measurements we were confident that the weight-data (Table 3) were reasonable (results are available in the Supplementary Material).

### Physical environment

Temperature and salinity profiles from CTD casts from the respective sampling stations were available for most of the dataset. Samples were classified as Atlantic ( $T > 3^\circ\text{C}$ ), Arctic ( $T < 0^\circ\text{C}$ ), or mixed ( $0^\circ\text{C} < T < 3^\circ\text{C}$ ) based on temperature at 50 m, where the core of Arctic water is usually found (Lind and Ingvaldsen, 2012; Lind *et al.*, 2016). Temperature and salinity at 50 m were used as continuous variables in the statistical analyses explaining variance in *Calanus* sp. biomass (see ii below), and sampling depth as a proxy for bottom depth since some samples were not taken from bottom to surface.

### Data analyses

Statistical analyses were performed to:

- (i) Estimate the relationship between *Calanus* biomass (sum of the three species) and the mesozooplankton biomass in the pair-wise samples.

- (ii) Evaluate interspecific differences in biomass between the three *Calanus* species with regard to key environmental drivers.
- (iii) Analyse inter-annual changes in the *Calanus* species group regarding species biomass and % contribution to total biomass.

For (i) and (ii), we employed the complete dataset with 616 samples (613 samples in (ii) due to missing temperature data from three stations). For (iii), we used summer and autumn data from region West (mainly FB transect) where we had annual observations since 1995. Analyses were performed on log-transformed estimated dw biomass plus a constant (0.01) to enable log-transformation of samples with species absence (zero biomass).

### Total *Calanus* vs. mesozooplankton biomass

We used Major Axis regression (MA) to estimate the relationship between the observed (log-transformed) mesozooplankton biomass and the estimated total biomass of *Calanus* spp. This regression technique is suitable for describing the functional relationship between two variables of the same units of measurement when both are subject to observation error (Helsel and Hirsch, 1992; Sokal and Rohlf, 2012). We also performed an ordinary least squares (OLS) regression for comparison with the MA, to

evaluate how results would change by the choice of regression model.

### Calanus biomass at species level

OLS regressions with species biomass as response variable was used to evaluate interspecific differences between the *Calanus* species with regard to environmental factors (temperature, salinity and sampling depth as continuous variables, season as categorical). Data on *C. glacialis* and *C. hyperboreus* had considerable zero-inflations as a large portion of the data came from the Atlantic sector of the Barents Sea, so analyses for these species were performed on all samples as well as only presence-data. We also ran separate analyses with presence/absence as a response, using Generalized Linear Models with a binomial distribution.

Model selection (i.e. deciding on the optimal models describing estimated biomass at species level) was based on the Akaike information criterion (AIC; Akaike, 1974) which considers the trade-off between model fit and model complexity, and backwards selection (stepwise removal of the least significant term).

All analyses were run both on the complete dataset and on data only including samples taken from bottom to surface. To account for differences in sampling gear characteristics like mesh size and net opening, equipment was included as a fixed covariate in the analyses. Due to an overweight of samples from the WP2 sampling gear, this dataset was not suitable for concluding on differences in sampling gear performance.

### Temporal changes in region West

Changes in biomass at species level and changes in the proportion of *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus* in the total mesozooplankton biomass over the period (1995–2016) were analysed with generalized additive models (GAMs) to catch potential non-linear trends in temporal variation. We used a spline based smoother with four degrees of freedom. In analyses of proportions, estimates >1 were set to 1, and analyses were run on arcsine transformed values.

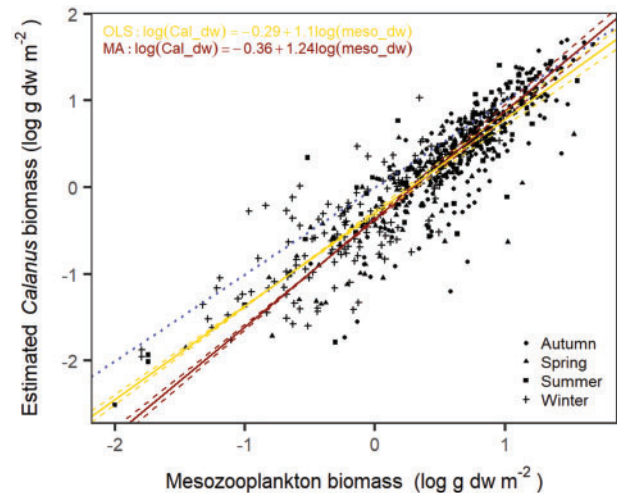
All analyses were done in the statistical software package R (R Core Team, 2016), using the mgcv library for GAMs (Wood, 2017).

## Results

### Correlation between *Calanus* spp. and total mesozooplankton biomass

There was a strong correlation between the observed mesozooplankton biomass and the estimated biomass of *Calanus* species in the samples ( $r^2 = 0.79$ ,  $p = 0.005$ ) (Figure 3). Results were similar both with the complete dataset and when excluding samples that did not cover the entire water column. The observed biomass spanned a range of about three orders of magnitude, from 0.01 to 48 g dw m<sup>-2</sup>, with a similar range also for the estimated biomass of *Calanus* species (0.003–50 g dw m<sup>-2</sup>). On average, the *Calanus* species comprised 78% of the mesozooplankton biomass, though this varied between the different regions (see below).

The scatter around the regression line in Figure 3 was approximately one order of magnitude (corresponding to one unit on the log scale). The estimated dw of the three *Calanus* spp. surpassed the observed mesozooplankton dw sampled at the station (i.e. observations above the 1:1 dotted line in Figure 3) in 19% of the cases. Overestimations occurred in all seasons, both at high and low biomass levels.



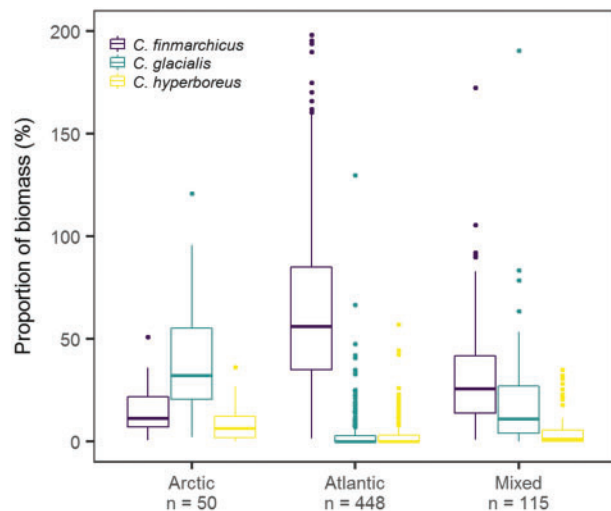
**Figure 3.** Observed mesozooplankton biomass and estimated total biomass of three *Calanus* species in the samples. Samples are shown with symbols by season; winter (November–March), spring (April–May), summer (June–July), and autumn (August–October). The dotted line shows a 1:1 relationship between mesozooplankton and *Calanus* spp. biomass. Regression results (MA and OLS) are plotted with 95% confidence bands,  $r^2 = 0.79$  and  $p = 0.005$  for both regressions.

The MA regression slope was steeper than unity (1.24 on the log-log scale), which means that the % contribution of *Calanus* species to the observed biomass increased with increasing biomass values. In fact, the regression line crossed the 1:1 line at a log value about 1.5 (32 g dw m<sup>-2</sup>). The OLS regression had a lower slope (1.1) and did not cross the 1:1 line. OLS in bivariate regressions tends to underestimate the slope of the regression line when both variables are subject to observation error not controlled by the researcher (Sokal and Rohlf, 2012), which may be reflected in our data as well (Figure 3). We therefore conclude that predictions from the MA regression more accurately described the relationship between *Calanus* spp. and mesozooplankton biomass in the Barents Sea.

### Hydrographic and spatial differences between *Calanus* spp.

There was considerable variation in the estimated % contribution of each species to mesozooplankton biomass in the water masses defined as Arctic, Atlantic and mixed (large interquartile ranges, Figure 4). However, the water masses were distinctively different regarding which of the three *Calanus* species that contributed to the mesozooplankton biomass. In Atlantic water, *C. finmarchicus* constituted a large part of the mesozooplankton biomass whereas *C. glacialis* had a low contribution to the total. In Arctic water *C. glacialis* prevailed, with low contribution by *C. finmarchicus*. Both *C. finmarchicus* and *C. glacialis* contributed to the total in mixed water masses. *Calanus hyperboreus* was generally a small part of the mesozooplankton biomass in all water masses, though relatively more abundant in the Arctic than the other two.

A summary of biomass estimates and estimated proportions of the three *Calanus* species in the five regions shown in Figure 1 is available in the Supplementary Material (Supplementary Table S2). The total contribution by the three *Calanus* species to the



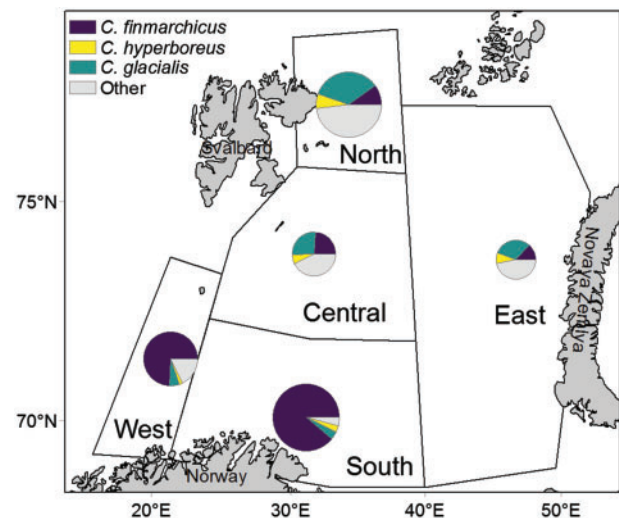
**Figure 4.** Estimated proportions of total mesozooplankton biomass for *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus* in different water masses defined as Atlantic ( $T > 3^{\circ}\text{C}$ ), Arctic ( $T < 0^{\circ}\text{C}$ ), and mixed ( $0^{\circ}\text{C} < T < 3^{\circ}\text{C}$ ). Number of samples ( $n$ ) from each water mass is indicated in the x-axis labels. The graph presented excludes 12 observations with estimated proportions  $>200\%$ . The boxes are divided by the median value, and framed by the upper and lower quartile. The whiskers extend to the first outlier in each direction; other outliers are shown by separate points. Outliers are defined as data points  $>1.5$  times the upper quartile.

mesozooplankton biomass differed across the regions, from  $\sim 50\%$  in the East to  $>90\%$  in the South. On species level, the % contribution in each area reflected differences between the water masses as illustrated in Figure 4. The West and South regions where Atlantic water prevails was dominated by *C. finmarchicus*, while *C. glacialis* was a larger fraction of the total in the North and East regions where Arctic water is present (Figure 5). Both species had a similar contribution to the biomass in the Central region which contains the oceanographic polar front with cooled Atlantic and mixed water masses. Species other than *Calanus* appeared to have a larger contribution to the mesozooplankton biomass in the North, Central and East regions than in the West and South (Figure 5). The “other” category is usually dominated by species like *Metridia* spp., *Pseudocalanus* spp., *Microcalanus* spp., *Oithona* spp., *Oncaea* spp., and *Clione limacina* (IMR database).

The total variation in estimated biomass within the pooled datasets was large, with coefficient of variation (CV) typically greater than one (Supplementary Table S2). CV values tended to be higher at low estimated biomass values and were generally higher for *Calanus* biomass estimates than for the total mesozooplankton biomass. High CV values suggest a skewed distribution (relative to normal) which is reflected in median values being lower than arithmetic means (by 5–40% for total mesozooplankton biomass, and 20–60% for estimated biomass of *C. finmarchicus* and *C. glacialis*).

#### Environmental drivers of *Calanus* biomass

Selected linear regressions based on the AIC and backwards selection, showed that the best model for describing the estimated biomass at species level included season, sampling depth, equipment and

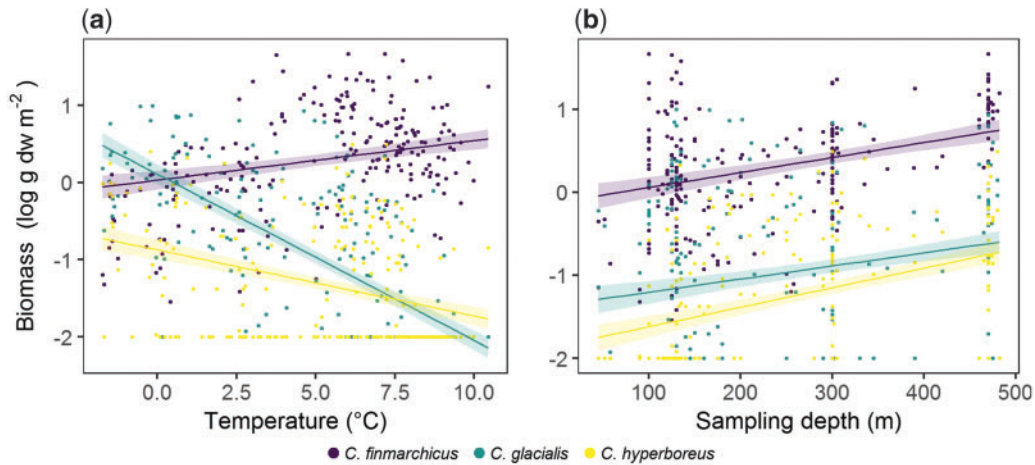


**Figure 5.** Estimated proportion of *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus* to total mesozooplankton biomass in different regions of the Barents Sea, based on arithmetic means ( $\text{g dw m}^{-2}$ ) per region. The size of the cakes is proportional to the total mesozooplankton biomass. “Other” represents the total minus the estimated mean biomass of the *Calanus* species. Winter samples from region West are not included in the figure.

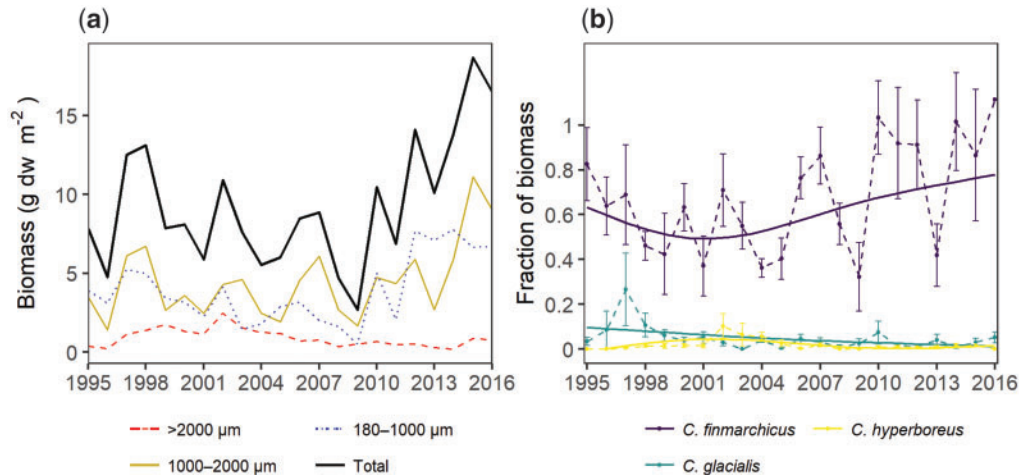
temperature (50 m) for all three species ( $r^2 = 0.38$  for *C. finmarchicus*, 0.51 for *C. glacialis* and 0.31 for *C. hyperboreus*). Model coefficients with standard errors are available in the Supplementary Table S3. Among the predictors, temperature revealed clear differences between the species (Figure 6a). *Calanus finmarchicus* had a positive relationship with temperature ( $p < 0.001$ ), while it was negative for *C. glacialis* ( $p < 0.001$ ). Also *C. hyperboreus* had a negative relationship with temperature ( $p < 0.001$ ), though weaker than for *C. glacialis*. Sampling depth was positively related to estimated biomass for all three species (Figure 6b), giving higher *Calanus* spp. biomass in deep vs. shallow water. The model for *C. finmarchicus* predicted a higher mean biomass in summer compared with autumn, and lower for winter and spring. For *C. glacialis* and *C. hyperboreus*, the models predicted lower mean biomass in winter, spring and summer compared with autumn. Salinity had no significant effect for neither species. These trends were consistent across all datasets (complete, bottom to surface and presence-only data for *C. glacialis* and *C. hyperboreus*). Further, binomial models on presence/absence for *C. glacialis* and *C. hyperboreus* confirmed the negative relationship of these species with temperature.

#### Temporal changes in region West

The total mesozooplankton biomass in June and August in region West showed an increasing trend in recent years (Figure 7a). This coincided with an increase in the medium (1000–2000  $\mu\text{m}$ ) and small (180–1000  $\mu\text{m}$ ) mesozooplankton size fractions, while the large ( $>2000 \mu\text{m}$ ) size fraction has decreased since around 2002. GAM analyses on the estimated proportion of the three *Calanus* species in the corresponding samples revealed a linear decrease in the % contribution to total biomass of *C. glacialis* over the period (Figure 7b,  $p = 0.04$ ). Meanwhile, the proportion of *C. finmarchicus* has increased since the early 2000s ( $p = 0.003$ ). *C. hyperboreus* constituted a very small part of the mesozooplankton biomass in region West. Its contribution to the total was generally below 5%



**Figure 6.** Estimated biomass of the three *Calanus* species against (a) temperature and (b) sampling depth, with data from equipment WP2 and season autumn. Predictions (straight lines with 95 % confidence bands) are from the linear models  $\log(\text{Calanus sp. dw}) \sim \text{temperature} + \text{season} + \text{depth} + \text{equipment}$  ( $r^2 = 0.38$  for *C. finmarchicus*, 0.52 for *C. glacialis*, and 0.31 for *C. hyperboreus*), with mean levels of depth (a) and temperature (b).



**Figure 7.** (a) Mean sampled June and August mesozooplankton biomass ( $\text{g dw m}^{-2}$ ) in the Barents Sea, region West, from 1995 to 2016. Figure shows total biomass and biomass divided into three size fractions. (b) Mean estimated proportion (%) of *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus* in the corresponding samples. Error bars show  $\pm$  the SEM proportion. One potential outlier with estimated proportion of *C. finmarchicus* >500 % was removed in the figure. The trend lines are results from GAM models with species proportions as response and year as explanatory variable;  $p = 0.003$ , 0.04, and 0.002 for *C. finmarchicus*, *C. glacialis* and *C. hyperboreus*, and deviance explained is 10, 4.2, and 12%, respectively.

except between the years 2002 and 2004 when it had a “peak” contribution (Figure 7b,  $p = 0.002$ ). Model outputs are available in the Supplementary Figure S1.

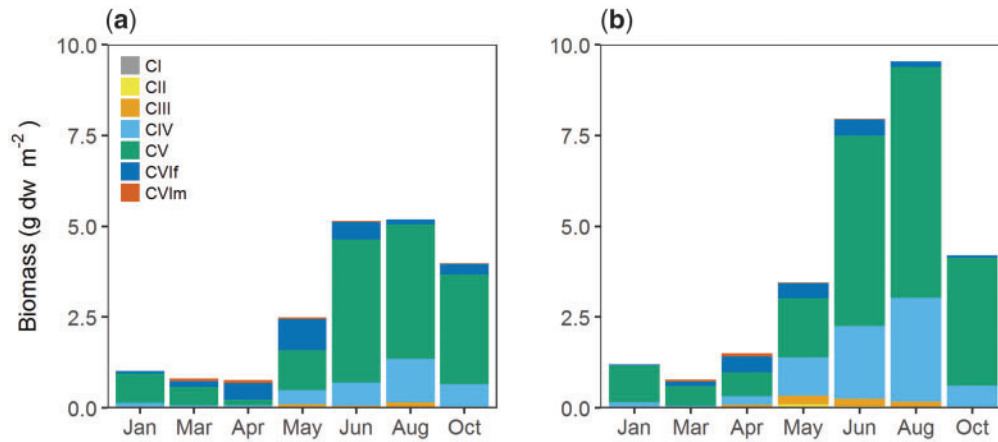
GAM analyses on estimated species biomass over the same period showed increasing biomass of *C. finmarchicus* since around 2005 ( $p = 0.05$ ) (see Figure 8b). At the same time, the biomass of *C. glacialis* decreased (apart from the most recent years), though the trend was not significant at the 0.05 level ( $p = 0.07$ ).

### Stage specific contribution to biomass

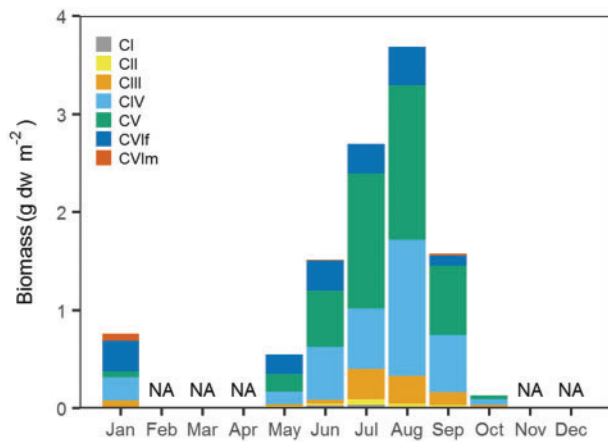
*Calanus finmarchicus* was a consistently large part of the mesozooplankton biomass in region West, where Atlantic

water dominates. Samples from this region revealed that copepodite stages CIV and CV dominated the total species biomass for *C. finmarchicus* (Figure 8). The new generation consisting of younger copepodites (CI–CIII) appeared in May. However, they comprised a very small part of the estimated total biomass in all months analysed. Stages CIV and CV of the new generation created a seasonal maximum biomass in June–August. Samples from winter months (January, March) indicated that *C. finmarchicus* overwinters mainly as stage CV in this area.

Stages CIV and CV dominated the biomass also for *C. glacialis* in regions Central, North and East (Figure 9) where this species was a large fraction of the mesozooplankton biomass. Winter samples for *C. glacialis* indicated overwintering mainly as stage



**Figure 8.** Mean biomass (g dw m<sup>-2</sup>) per stage (CI to CV and CVI female and male) for *C. finmarchicus* in the western region of the Barents Sea between (a) 1995–2004 and (b) 2005–2016. The figure only displays months which have been consistently sampled over the period.



**Figure 9.** Mean biomass (g dw m<sup>-2</sup>) per stage (CI to CV and CVI female and male) for *C. glacialis*, with data from the Central, North and East regions considered as most representative for this species. Months with no observations are indicated by NA.

CIV and adults. The younger stages, particularly CIII, had a larger contribution to the total species biomass for *C. glacialis* during summer and autumn than with *C. finmarchicus*. The maximum mean monthly estimated biomass of *C. glacialis* of about 3.6 g dw m<sup>-2</sup> was comparable to (but slightly lower than) the maximum biomass of *C. finmarchicus* apart from the higher values for the latter species after 2005 (Figure 8b).

## Discussion

### Estimated biomass of *Calanus* species

*Calanus* spp. are key species at high latitudes spanning from boreal to Arctic ecosystems (Jaschnov, 1970; Conover, 1988; Falk-Petersen *et al.*, 2009). Yet, few studies have quantified the contribution of *Calanus* species to the total zooplankton biomass. Biomass of *Calanus* is typically estimated by combining stage-abundance data with mean individual body weights of the respective stages (e.g. Tande, 1991; Hirche and Kosobokova, 2003; Søreide *et al.*, 2008). Using this method, we found a mean biomass of *C. finmarchicus* around 5 g dw m<sup>-2</sup> in June and August (1995–2005) in the western region of the Barents Sea dominated

by Atlantic water. After 2005, the biomass of *C. finmarchicus* has increased. Our estimates for the later years (2005–2016) are in the high end of the range of values reported from other areas. A detailed sampling at Station M in the Norwegian Sea gave a mean biomass of 1.7 g dw m<sup>-2</sup> with a temporary maximum of 12.5 g dw m<sup>-2</sup> (Hirche *et al.*, 2001). Simulations with a coupled physical–biological model system (NORWECOM) gave a seasonal maximum biomass of *C. finmarchicus* of 4–5 g dw m<sup>-2</sup> in the Norwegian Sea and the Atlantic part of the Barents Sea (Hjøllo *et al.*, 2012; Skaret *et al.*, 2014, see review of estimated biomass of the three *Calanus* species provided in the Supplementary Table S4). Our estimates for the colder waters of the central, eastern and northern Barents Sea were lower, and similar to values obtained in the same region by Hirche and Kosobokova (2003).

Estimated biomass of *C. glacialis* in the North, Central and East regions was slightly lower than the biomass of *C. finmarchicus* in the West, with a seasonal maximum around 3.6 g dw m<sup>-2</sup>. This is comparable to studies of *C. glacialis* both from the Barents Sea and other areas (Tande, 1991; Madsen *et al.*, 2001; Hirche and Kosobokova, 2003; Daase *et al.*, 2013). Our biomass estimates for *C. hyperboreus* were 0.1–0.7 g dw m<sup>-2</sup> as means for the different areas. These are similar to values reported from the Barents Sea by Tande (1991) and Hirche and Kosobokova (2003). Higher values of up to 4–6 g dw m<sup>-2</sup> have been reported from the Greenland Sea (Hirche, 1991; Møller *et al.*, 2006) and Disco Bay (Madsen *et al.*, 2001).

Misidentification of *Calanus* species from the use of fixed size limits (see “Materials and methods” section) may have influenced the results. The most frequent cases of misidentifications are small individuals of *C. glacialis* wrongly identified as *C. finmarchicus* (Gabrielsen *et al.* 2012). A hybrid species is expected to have intermediate prosome lengths (Parent *et al.*, 2012). Species distributions were in our study highly related to water masses; and in Atlantic water where *C. finmarchicus* dominated, the overall contribution by *C. glacialis* was low. Co-occurrence between *C. finmarchicus* and *C. glacialis* was more prominent in the mixed water masses, and here the potential for misidentification (and possible hybridization) may have been greater.

One could expect that increasing water temperatures in the Barents Sea would lead to decreasing size of *C. finmarchicus*



copepodites (Campbell *et al.*, 2001). Albeit a small sample size, the length measurements we performed as part of this study did in fact indicate that *C. finmarchicus* have become smaller between 1997 and 2010 (Supplementary Table S5). Smaller *C. finmarchicus* reduces the probability of overlapping in size with its congener *C. glacialis*. It is also reasonable to expect that warmer conditions would favour the dominance of *C. finmarchicus* (Kjellerup *et al.*, 2012). We therefore believe that the general trends we observe in this study would be consistent despite the possibilities of species misidentification (due to size overlap and possible hybridization) in our data.

### Variation in weights of *Calanus* copepodites

Variation in size (weight) can be a considerable source of error and uncertainty in *Calanus* biomass estimates from species counts. Our *Calanus* biomass estimates surpassed the observed total biomass in one out of five samples. Responding to the overestimations, we repeated species counts on a selection of samples (formalin preserved) from years with large discrepancies between estimated dw of *C. finmarchicus* and observed mesozooplankton biomass. The new measurements did, however, not reveal any abundance estimation errors that could explain the biomass overestimations. We believe the overestimations reflect uncertainties in the weight-at-stage data employed when estimating species biomass, as well as variance introduced by subsampling when estimating species abundances (see e.g. Skjoldal *et al.*, 2013).

Most studies where *Calanus* spp. biomass is estimated have used mean weights of copepodite stages from the literature. It is difficult to quantify the uncertainty, but from the variation in mean weights of the older copepodite stages shown in Figure 2 it may be of order 20–30% for *C. finmarchicus* and *C. glacialis*, or even larger. In some studies (e.g. Hirche *et al.*, 1991) the weights of individuals have been determined as part of the study, thereby reducing this uncertainty. Size measurements performed on representative material to reveal changes in mean weights over space and time would greatly improve the precision of biomass estimates from zooplankton species abundance data. This may, however, induce a considerable increase in the effort spent on sample analysis. Using some form of plankton-imaging-system (Benfield *et al.*, 2007) may facilitate the approach to make it more practical in routine studies.

### *Calanus* spp. as drivers of the mesozooplankton biomass in the Barents Sea

*Calanus finmarchicus*, *C. glacialis*, and *C. hyperboreus* are major players in the herbivore zooplankton community of the Barents Sea ecosystem. Our study has shown that *Calanus* species constitute a major part of the mesozooplankton biomass in all regions of the Barents Sea, and on average around 80% of the total. Large mesozooplankton biomass samples ( $>16$  g dw m<sup>-2</sup>) were associated with correspondingly large estimated biomass of *Calanus* species, indicating that biomass “peaks” in the Barents Sea are mainly driven by *Calanus* spp. The combined biomass of these species explained a major part of the variation in the observed mesozooplankton biomass. Though the total biomass of *Calanus* spp. contributed in similar proportion to the mesozooplankton biomass across the regions, the highest contribution was observed in regions West and South where there is a high abundance of *C. finmarchicus*. The proportional contribution of *C. glacialis* to the zooplankton biomass in its core Arctic water area was lower

than the contribution of *C. finmarchicus* in Atlantic water, and other species than *Calanus* seem to comprise a larger part of the mesozooplankton biomass here. The larger species *C. hyperboreus* had a rather low contribution to the mesozooplankton biomass ( $<10\%$  in all regions), similar to earlier observations (Melle and Skjoldal, 1998; Arashkevich *et al.*, 2002; Hirche and Kosobokova, 2003). *Calanus hyperboreus* generally overwinters below 500–1000 m in its core areas (Hirche, 1997), and has probably difficulties in completing a generation cycle in the (relatively shallow) Barents Sea due to its large size and longer life-span making it more vulnerable to predation (e.g. Falk-Petersen *et al.*, 2009; Berge *et al.*, 2012).

Our data showed that the contribution of *Calanus* to the mesozooplankton biomass is lower when the total zooplankton biomass is low (see regression in Figure 3). Considering that a major part of our data was from Atlantic water areas, we believe part of this result can be explained by a seasonal/advective effect of *C. finmarchicus*. During winter when the mesozooplankton biomass is low, there will be lower concentrations of *C. finmarchicus* in the inflowing Atlantic water when it has descended (over-winter in deep Norwegian Sea basins) from the surface layers of the advective Atlantic current (Skjoldal *et al.*, 1992). Hence, there will be a lower contribution of *Calanus* spp. to the total in winter vs. summer periods. A biological explanation is selective foraging by predators. The little auk *Alle alle* actively selects larger stages of *C. glacialis* when feeding in the Arctic, and avoids the smaller *C. finmarchicus* (Karnovsky *et al.*, 2003). Baltic herring has shown size-selective preferences when feeding on copepods (Sandström, 1980), and planktivore fish in the Barents Sea can exert a significant top-down control on their zooplankton prey (Hassel *et al.*, 1991; Stige *et al.*, 2014).

### *Calanus* spp. biomass and hydrography

Both this and previous studies (Tande, 1991; Melle and Skjoldal, 1998; Hirche and Kosobokova, 2003) have demonstrated that the contribution of *C. finmarchicus* and *C. glacialis* to the zooplankton biomass in the Barents Sea is highly related to which water mass dominates. Weydmann *et al.* (2014) described temperature and bottom depth as the main drivers for zooplankton variability in the West Spitsbergen Current. Daase *et al.* (2007) demonstrated similar temperature-relationships as our study for the *Calanus* species in waters off Svalbard, and related the findings to advective processes. The steep, negative biomass-temperature relationship of *C. glacialis* in our study reflected large difference in biomass of *C. glacialis* in Arctic vs. Atlantic water masses.

The area of Arctic water in the Barents Sea has been declining over the last few decades (ICES, 2017). This could possibly be associated with a reduction in the habitat (extent and conditions) of *C. glacialis* in the northern Barents Sea. It has been suggested that *C. glacialis* will decrease in Arctic areas of the Barents Sea if continuous warming leads to a greater mismatch between phytoplankton production and *C. glacialis* development due to earlier break-up of the winter ice (Hirche and Kosobokova, 2007; Søreide *et al.*, 2010). The decrease of this species at the southwestern entrance (region West) could reflect a general decline in the core area further north. However, our data from the northern Barents Sea are limited ( $n=23$ ; Tables 2) and too heterogenous in time to allow us to examine if this has been the case. This is an important issue from an ecosystem perspective which we plan to

address in a future study, using archived samples dating back to the 1980s.

*Calanus finmarchicus* is an expatriate in Arctic water masses, and its reproductive cycle is limited by the low temperature environment (Melle and Skjoldal, 1998; Hirche and Kosobokova, 2007; Ji *et al.*, 2012). Previous studies have also established a positive relationship between *C. finmarchicus* biomass and temperature (Dalpadado *et al.*, 2003; Daase *et al.* 2007; Dvoretzky, 2011). High temperatures may indicate higher inflow of Atlantic water and thus larger concentrations of advective organisms like *C. finmarchicus* (Dalpadado *et al.*, 2003). Furthermore, *C. finmarchicus* has higher growth rates (Campbell *et al.*, 2001) and augmented egg production (Kjellerup *et al.*, 2012) at increasing temperatures. The optimum temperature for this species appears to be about 6–10 °C based on abundance data over its geographical range (Helaouët and Beaugrand, 2007; Helaouët *et al.*, 2011; Reygondeau and Beaugrand, 2011; Melle *et al.*, 2014). The temperature of the inflowing Atlantic water at the FB transect has been increasing by about 1.5 °C since around 1980 to an annual mean level of about 6–6.5 °C after 2004 (Eriksen *et al.*, 2017b). This may have improved the conditions and expanded the optimal habitat for *C. finmarchicus* in the southern Barents Sea.

The number of generations produced per year by boreal *Calanus* decreases with increasing latitude (Conover, 1988). Though previous studies have suggested that *C. finmarchicus* produces one generation per year in the Barents Sea (e.g. Tande *et al.*, 1985; Melle and Skjoldal, 1998), there are indications for a second generation of *C. finmarchicus*, particularly related to warm periods (Timofeev, 2000; Skaret *et al.*, 2014). A second generation of *C. finmarchicus* may have contributed to the marked increase in biomass of *C. finmarchicus* in region West during the most recent period analysed here (after 2005).

Coupled with the decrease in Arctic water masses in the Barents Sea is an increase of mixed water with intermediate temperatures of 0–3 °C (Eriksen *et al.* 2017b). Related to the issue of whether *C. glacialis* has declined as a response to the ongoing warming is therefore also a question of how the *Calanus* species are coping with the conditions in the mixed water masses. Temperature-driven stage-duration coupled with food availability and the length of the growth season in these waters, will largely determine the ability of *C. finmarchicus* to reach diapausing stage over the season (e.g. Ji *et al.*, 2012). *Calanus glacialis* should persist physiologically at these cool temperatures, as suggested by its dominance in the White Sea (Kosobokova, 1999), though it is an open question as to how changes in ice conditions and water masses will affect the species in the mixed waters. Model predictions by Slagstad *et al.* (2011) have suggested that the secondary production by *C. glacialis* and *C. finmarchicus* combined will decrease in a future warmer climate in the northern Barents Sea, due to a temperature regime that is too warm for *C. glacialis* and sub-optimal for *C. finmarchicus*.

### Concluding remarks

Plankton are good indicators of climate change occurring in the oceans (Hays *et al.*, 2005). We have shown that the recent warming in the Barents Sea is likely affecting the composition of the mesozooplankton community, increasing the abundance of Atlantic *C. finmarchicus* in the west. With increased inflow of Atlantic water into the system, we would not expect these changes to be restricted only to the western area, as both fish species and macrozooplankton have shown responses to the warming in

extended areas of the Barents Sea (Fossheim *et al.*, 2015; Eriksen *et al.*, 2017b, Frainer *et al.* 2017). A transition in the mesozooplankton community in certain areas from dominance of *C. glacialis* towards the smaller *C. finmarchicus* could be detrimental for higher trophic levels, particularly the size-selective particulate feeders (e.g. Karnovsky *et al.*, 2003; Hirche and Kosobokova, 2007). Consistent time-series like ours from the FB transect and from the joint Norwegian-Russian ecosystem survey in autumn (Eriksen *et al.* 2017a) are crucial for revealing ongoing changes in zooplankton communities. Progress of the *Calanus* species in a future, warmer Barents Sea, particularly changes towards dominance of smaller sized individuals over a larger geographical area, deserves high priority in future research considering the key role of these species in the ecosystem.

### Supplementary data

Supplementary material is available at the ICESJMS online version of the article.

### Acknowledgements

We acknowledge technicians, scientists and crew of the various research cruises at the Institute of Marine Research (IMR), Norway, who have participated over the years in collecting and processing mesozooplankton data utilized in our study. We thank two anonymous referees for valuable comments on an earlier version of the article. This study was funded by the Norwegian Research Council project TIBIA (Trophic interactions in the Barents Sea—steps towards an Integrated Ecosystem Assessment, No. 228880) at IMR.

### References

- Akaike, H. 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, 19: 716–723.
- Arashkevich, E., Wassmann, P., Pasternak, A., and Riser, C. W. 2002. Seasonal and spatial changes in biomass, structure, and development progress of the zooplankton community in the Barents Sea. *Journal of Marine Systems*, 38: 125–145.
- Båmstedt, U., and Ervik, A. 1984. Local variations in size and activity among *Calanus finmarchicus* and *Metridia longa* (Copepoda, Calanoida) overwintering on the west coast of Norway. *Journal of Plankton Research*, 6: 843–857.
- Båmstedt, U., and Tande, K. S. 1985. Respiration and excretion rates of *Calanus glacialis* in Arctic waters of the Barents Sea. *Marine Biology*, 87: 259–266.
- Beaugrand, G., Reid, P. C., Ibañez, F., Lindley, J. A., and Edwards, M. 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. *Science*, 296: 1692–1694.
- Beaugrand, G., Brander, K. M., Alistair Lindley, J., Souissi, S., and Reid, P. C. 2003. Plankton effect on cod recruitment in the North Sea. *Nature*, 426: 661–664.
- Benfield, M., Grosjean, P., Culverhouse, P., Irigolen, X., Sieracki, M., Lopez-Urrutia, A. *et al.* 2007. RAPID: research on automated plankton identification. *Oceanography*, 20: 172–187.
- Berge, J., Gabrielsen, T. M., Moline, M., and Renaud, P. E. 2012. Evolution of the Arctic *Calanus* complex: an Arctic marine avocado? *Journal of Plankton Research*, 34: 191–195.
- Boitsov, V. D., Karsakov, A. L., and Trofimov, A. G. 2012. Atlantic water temperature and climate in the Barents Sea, 2000–2009. *ICES Journal of Marine Science*, 69: 833–840.
- Campbell, R. G., Wagner, M. M., Teegarden, G. J., Boudreau, C. A., and Durbin, E. G. 2001. Growth and development rates of the copepod *Calanus finmarchicus* reared in the laboratory. *Marine Ecology Progress Series*, 221: 161–183.

- Carlotti, F., Krause, M., and Radach, G. 1993. Growth and development of *Calanus finmarchicus* related to the influence of temperature: experimental results and conceptual model. *Limnology and Oceanography*, 38: 1125–1134.
- 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.
- Daase, M., Vik, J. O., Bagøien, E., Stenseth, N. C., and Eiane, K. 2007. The influence of advection on *Calanus* near Svalbard: statistical relations between salinity, temperature and copepod abundance. *Journal of Plankton Research*, 29: 903–911.
- Daase, M., Falk-Petersen, S., Varpe, Ø., Darnis, G., Søreide, J. E., Wold, A., Leu, E. *et al.* 2013. Timing of reproductive events in the marine copepod *Calanus glacialis*: a pan-Arctic perspective. *Canadian Journal of Fisheries and Aquatic Sciences*, 70: 871–884.
- Dalpadado, P., Ingvaldsen, R., and Hassel, A. 2003. Zooplankton biomass variation in relation to climatic conditions in the Barents Sea. *Polar Biology*, 26: 233–241.
- Dalpadado, P., and Mowbray, F. 2013. Comparative analysis of feeding ecology of capelin from two shelf ecosystems, off Newfoundland and in the Barents Sea. *Progress in Oceanography*, 114: 97–105.
- Dalpadado, P., Arrigo, K. R., Hjøllø, S. S., Rey, F., Ingvaldsen, R. B., Sperfeld, E., van Dijken, G. L. *et al.* 2014. Productivity in the Barents Sea - response to recent climate variability. *PLoS One*, 9: e95273.
- Diel, S. 1991. On the life history of dominant copepod species (*Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus*, *Metridia longa*) in the Fram Strait. *Reports on Polar Research*, 88: 1–113.
- Dvoretzky, V. G. 2011. Distribution of *Calanus* species off Franz Josef Land (Arctic Barents Sea). *Polar Science*, 5: 361–373.
- Eriksen, E., Skjoldal, H. R., Dolgov, A. V., Dalpadado, P., Orlova, E. L., and Prozorkevich, D. V. 2016. The Barents Sea euphausiids: methodological aspects of monitoring and estimation of abundance and biomass. *ICES Journal of Marine Science*, 73: 1533–1544.
- Eriksen, E., Gjørseter, H., Prozorkevich, D., Shamray, D., Dolgov, A., Skern-Mauritzen, M., Stiansen, J. E. *et al.* 2017a. From single species surveys towards monitoring of the Barents Sea ecosystem. *Progress in Oceanography* (in press). <http://www.sciencedirect.com/pva.uib.no/science/article/pii/S0079661117300642>
- Eriksen, E., Skjoldal, H. R., Gjørseter, H., and Primicerio, R. 2017b. Spatial and temporal changes in the Barents Sea pelagic compartment during the recent warming. *Progress in Oceanography*, 151: 206–226.
- Falk-Petersen, S., Mayzaud, P., Kattner, G., and Sargent, J. 2009. Lipids and life strategy of Arctic *Calanus*. *Marine Biology Research*, 5: 18–39.
- Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R. B., Aschan, M. M., and Dolgov, A. V. 2015. Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nature Climate Change*, 5: 673–676.
- Fraïner, A., Primicerio, R., Kortsch, S., Aune, M., Dolgov, A. V., Fossheim, M., and Aschan, M. M. 2017. Climate-driven changes in functional biogeography of Arctic marine fish communities. *Proceedings of the National Academy of Sciences of the United States of America*, 114: 12202–12207.
- Gabrielsen, T. M., Merkel, B., Søreide, J. E., Johansson-Karlsson, E., Bailey, A., Vogedes, D., Nygård, H. *et al.* 2012. Potential misidentifications of two climate indicator species of the marine arctic ecosystem: *Calanus glacialis* and *C. finmarchicus*. *Polar Biology*, 35: 1621–1628.
- Gislason, A. 2005. Seasonal and spatial variability in egg production and biomass of *Calanus finmarchicus* around Iceland. *Marine Ecology Progress Series*, 286: 177–192.
- Hanssen, H. 1997. Mesozooplankton of the Laptev Sea and the adjacent eastern Nansen Basin—distribution and community structure in late summer. *Berichte zur Polarforschung*, 229: 1–131.
- Hassel, A. 1986. Seasonal changes in zooplankton composition in the Barents Sea, with special attention to *Calanus* spp. (Copepoda). *Journal of Plankton Research*, 8: 329–339.
- Hassel, A., Skjoldal, H. R., Gjørseter, H., Loeng, H., and Omli, L. 1991. Impact of grazing from capelin (*Mallotus villosus*) on zooplankton: a case study in the northern Barents Sea in August 1985. *Polar Research*, 10: 371–388.
- Hays, G. C., Richardson, A. J., and Robinson, C. 2005. Climate change and marine plankton. *Trends in Ecology and Evolution*, 20: 337–344.
- Heath, M. R., and Jónasdóttir, S. H. 1999. Distribution and abundance of overwintering *Calanus finmarchicus* in the Faroe–Shetland Channel. *Fisheries Oceanography*, 8: 40–60.
- Helaouët, P., and Beaugrand, G. 2007. Macroecology of *Calanus finmarchicus* and *C. helgolandicus* in the North Atlantic Ocean and adjacent seas. *Marine Ecology Progress Series*, 345: 147–165.
- Helaouët, P., Beaugrand, G., and Reid, P. C. 2011. Macrophysiology of *Calanus finmarchicus* in the North Atlantic Ocean. *Progress in Oceanography*, 91: 217–228.
- Helsel, D. R., and Hirsch, R. M. 1992. *Statistical Methods in Water Resources*. Studies in Environmental Science. Elsevier, Amsterdam.
- Hirche, H. 1987. Temperature and plankton. *Marine Biology*, 94: 347–356.
- Hirche, H. J. 1991. Distribution of dominant calanoid copepod species in the Greenland Sea during late fall. *Polar Biology*, 11: 351–362.
- Hirche, H. J. 1997. Life cycle of the copepod *Calanus hyperboreus* in the Greenland Sea. *Marine Biology*, 128: 607–618.
- Hirche, H. J., and 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: 615–622.
- Hirche, H. J., and Kosobokova, K. 2003. Early reproduction and development of dominant calanoid copepods in the sea ice zone of the Barents Sea—need for a change of paradigms? *Marine Biology*, 143: 769–781.
- Hirche, H. J., and Kosobokova, K. 2007. Distribution of *Calanus finmarchicus* in the northern North Atlantic and Arctic Ocean—Expatriation and potential colonization. *Deep Sea Research Part II: Topical Studies in Oceanography*, 54: 2729–2747.
- Hirche, H. H., and Kwasniewski, S. 1997. Distribution, reproduction and development of *Calanus* species in the Northeast Water in relation to environmental conditions. *Journal of Marine Systems*, 10: 299–317.
- Hirche, H. J., and Mumm, N. 1992. Distribution of dominant copepods in the Nansen Basin, Arctic Ocean, in summer. *Deep Sea Research Part A. Oceanographic Research Papers*, 39: 485–505.
- Hirche, H., Baumann, M. E. M., Kattner, G., and Gradinger, R. 1991. Plankton distribution and the impact of copepod grazing on primary production in Fram Strait, Greenland Sea. *Journal of Marine Systems*, 2: 477–494.
- Hirche, H., Brey, T., and Niehoff, B. 2001. A high-frequency time series at Ocean Weather Ship Station M (Norwegian Sea): population dynamics of *Calanus finmarchicus*. *Marine Ecology Progress Series*, 219: 205–219.
- Hirche, H., Hagen, W., Mumm, N., and Richter, C. 1994. The Northeast Water polynya, Greenland Sea III. Meso- and macrozooplankton distribution and production of dominant herbivorous copepods during spring. *Polar Biology*, 14: 491–503.
- Hjøllø, S. S., Huse, G., Skogen, M. D., and Melle, W. 2012. Modelling secondary production in the Norwegian Sea with a fully coupled

- physical/primary production/individual-based *Calanus finmarchicus* model system. *Marine Biology Research*, 8: 508–526.
- ICES. 2017. Report of the Working Group on the Integrated Assessments of the Barents Sea (WGIBAR), 16–18 March 2017. ICES CM 2017/SSGIEA: 04.
- Ikeda, T., and Skjoldal, H. R. 1989. Metabolism and elemental composition of zooplankton from the Barents Sea during early Arctic summer. *Marine Biology*, 100: 173–183.
- 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.
- Ji, R., Ashjian, C. J., Campbell, R. G., Chen, C., Gao, G., Davis, C. S., Cowles, G. W., and Beardsley, R. C. 2012. Life history and biogeography of *Calanus* copepods in the Arctic Ocean: an individual-based modeling study. *Progress in Oceanography*, 96: 40–56.
- Jónasdóttir, S. H. 1999. Lipid content of *Calanus finmarchicus* during overwintering in the Faroe–Shetland Channel. *Fisheries Oceanography*, 8: 61–72.
- Karnovsky, N., Kwasniewski, S., Weslawski, J., Walkusz, W., and Beszczynska-Möller, A. 2003. Foraging behavior of little auks in a heterogeneous environment. *Marine Ecology Progress Series*, 253: 289–303.
- Kjellerup, S., Dunweber, M., Swalethorp, R., Nielsen, T. G., Møller, E. F., Markager, S., and Hansen, B. W. 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.
- Kosobokova, K. N. 1999. The reproductive cycle and life history of the Arctic copepod *Calanus glacialis* in the White Sea. *Polar Biology*, 22: 254–263.
- Knutsen, T., and Dalpadado, P. 2009. Økosystem barentshavet. In *Havets ressurser og miljø 2009*, pp 185. Ed. by H. Gjøsæter. Institute of Marine Research, Bergen. <http://hdl.handle.net/11250/116992>.
- Kvile, K. O., Fiksen, O., Prokopchuk, I., and Opdal, A. F. 2017. Coupling survey data with drift model results suggests that local spawning is important for *Calanus finmarchicus* production in the Barents Sea. *Journal of Marine Systems*, 165: 69–76.
- Lee, R. F. 1975. Lipids of Arctic zooplankton. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology*, 51: 263–266.
- Lind, S., and Ingvaldsen, R. B. 2012. Variability and impacts of Atlantic Water entering the Barents Sea from the north. *Deep-Sea Research Part I: Oceanographic Research Papers*, 62: 70–88.
- Lind, S., Ingvaldsen, R. B., and Furevik, T. 2016. Arctic layer salinity controls heat loss from deep Atlantic layer in seasonally ice-covered areas of the Barents Sea. *Geophysical Research Letters*, 43: 5233–5242.
- Madsen, S. D., Nielsen, T. G., and Hansen, B. W. 2001. Annual population development and production by *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* in Disko Bay, western Greenland. *Marine Biology*, 139: 75–93.
- Melle, W., and Skjoldal, H. R. 1998. Reproduction and development of *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* in the Barents Sea. *Marine Ecology Progress Series*, 169: 211–228.
- Melle, W., Ellertsen, B., and Skjoldal, H. R. 2004. Zooplankton: the link to higher trophic levels. In *The Norwegian Sea Ecosystem*, pp. 137–202. Ed. by H. R. Skjoldal. Tapir Academic Press, Trondheim.
- Melle, W., Runge, J., Head, E., Plourde, S., Castellani, C., Licandro, P., Pierson, J. *et al.* 2014. The North Atlantic Ocean as habitat for *Calanus finmarchicus*: Environmental factors and life history traits. *Progress in Oceanography* 129: 244–284.
- Møller, E. F., Nielsen, T. G., and Richardson, K. 2006. The zooplankton community in the Greenland Sea: Composition and role in carbon turnover. *Deep Sea Research Part I: Oceanographic Research Papers*, 53: 76–93.
- Orlova, E., Dalpadado, P., Knutsen, T., Nesterova, V. N., and Prokopchuk, I. P. 2011. Zooplankton. In *The Barents Sea - Ecosystem, Resources, Management. Half a Century of Russian-Norwegian Cooperation*, pp. 91–119. Ed. by T. Jakobsen and V. K. Ožigin. Tapir Academic Press, Trondheim.
- Parent, G. J., Plourde, S., and Turgeon, J. 2011. Overlapping size ranges of *Calanus* spp. off the Canadian Arctic and Atlantic Coasts: impact on species' abundances. *Journal of Plankton Research*, 33: 1654–1665.
- Parent, G. J., Plourde, S., and Turgeon, J. 2012. Natural hybridization between *Calanus finmarchicus* and *C. glacialis* (Copepoda) in the Arctic and Northwest Atlantic. *Limnology and Oceanography*, 57: 1057–1066.
- R Core Team. 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Reygondeau, G., and Beaugrand, G. 2011. Future climate-driven shifts in distribution of *Calanus finmarchicus*. *Global Change Biology*, 17: 756–766.
- Runge, J. A., Plourde, S., Joly, P., Niehoff, B., and Durbin, E. 2006. Characteristics of egg production of the planktonic copepod, *Calanus finmarchicus*, on Georges Bank: 1994–1999. *Deep Sea Research Part II: Topical Studies in Oceanography*, 53: 2618–2631.
- Sakshaug, E., Johnsen, G., and Kovacs, K. 2009. *Ecosystem Barents Sea*. Tapir Academic Press, Trondheim.
- Sameoto, D., Wiebe, P. H., Runge, J., Postel, L., Dunn, J., Miller, C., and Coombs, S. 2000. Collecting zooplankton. In *ICES Zooplankton Methodology Manual*, pp. 55–82. Ed. by R. Harris, P. H. Wiebe, J. Lenz, H. R. Skjoldal, and M. Huntley. Academic Press, San Diego.
- Scott, C. L., Kwasniewski, S., Falk-Petersen, S., and Sargent, J. R. 2000. Lipids and life strategies of *Calanus finmarchicus*, *Calanus glacialis* and *Calanus hyperboreus* in late autumn, Kongsfjorden, Svalbard. *Polar Biology*, 23: 510–516.
- Skaret, G., Dalpadado, P., Hjøllo, S. S., Skogen, M. D., and Strand, E. 2014. *Calanus finmarchicus* abundance, production and population dynamics in the Barents Sea in a future climate. *Progress in Oceanography*, 125: 26–39.
- Skjoldal, H. R., Gjøsæter, H., and Loeng, H. 1992. The Barents Sea ecosystem in the 1980s: ocean climate, plankton, and capelin growth. *ICES Marine Science Symposium*, 195: 278–290.
- Skjoldal, H. R., Wiebe, P. H., Postel, L., Knutsen, T., Kaartvedt, S., and Sameoto, D. D. 2013. Intercomparison of zooplankton (net) sampling systems: Results from the ICES/GLOBEC sea-going workshop. *Progress in Oceanography*, 108: 1–42.
- Slagstad, D., Ellingsen, I. H., and Wassmann, P. 2011. Evaluating primary and secondary production in an Arctic Ocean void of summer sea ice: An experimental simulation approach. *Progress in Oceanography*, 90: 117–131.
- Smedsrud, L. H., Esau, I., Ingvaldsen, R. B., Eldevik, T., Haugan, P. M., Li, C., Lien, V. S., Olsen, A., Omar, A. M., Otterå, O. H., *et al.* 2013. The role of the Barents Sea in the Arctic climate system. *Reviews of Geophysics*, 51: 415–449.
- Sokal, R. R., and Rohlf, F. J. 2012. *Biometry - The Principles and Practice of Statistics in Biological Research*. W. H. Freeman and Company, New York.
- Søreide, J. E., Falk-Petersen, S., Hegseth, E. N., Hop, H., Carroll, M. L., Hobson, K. A., and Blachowiak-Samolyk, K. 2008. Seasonal feeding strategies of *Calanus* in the high-Arctic Svalbard region. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 55: 2225–2244.
- Søreide, J. E., Leu, E., Berge, J., Graeve, M., and Falk-Petersen, S. 2010. Timing of blooms, algal food quality and *Calanus glacialis* reproduction and growth in a changing Arctic. *Global Change Biology*, 16: 3154–3163.

- Stige, L. C., Dalpadado, P., Orlova, E., Boulay, A. C., Durant, J. M., Ottersen, G., and Stenseth, N. C. 2014. Spatiotemporal statistical analyses reveal predator-driven zooplankton fluctuations in the Barents Sea. *Progress in Oceanography*, 120: 243–253.
- Tande, K. S. 1982. Ecological investigations on the zooplankton community of Balsfjorden, northern Norway: Generation cycles, and variations in body weight and body content of carbon and nitrogen related to overwintering and reproduction in the copepod *Calanus finmarchicus* (Gunnerus). *Journal of Experimental Marine Biology and Ecology*, 62: 129–142.
- Tande, K. S. 1991. *Calanus* in the North Norwegian fjords and in the Barents Sea. *Polar Research*, 10: 389–407.
- Tande, K., Hassel, A., and 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*, pp. 141–155. Ed. by J. S. Gray and M. E. Christiansen. Wiley and Sons, New York.
- Tande, K. S., and Slagstad, D. 1992. Regional and interannual variations in biomass and productivity of the marine copepod, *Calanus finmarchicus*, in sub-arctic environments. *Oceanologica Acta*, 15: 309–321.
- Timofeev, S. 2000. *Ecology of the Marine Zooplankton*. Murmansk State Pedagogical Institute Press, Murmansk.
- Torgersen, T., and Huse, G. 2005. Variability in retention of *Calanus finmarchicus* in the Nordic Seas. *ICES Journal of Marine Science*, 62: 1301–1309.
- Tourangeau, S., and Runge, J. A. 1991. Reproduction of *Calanus glacialis* under ice in spring in southeastern Hudson Bay, Canada. *Marine Biology*, 108: 227–233.
- Unstad, K. H., and Tande, K. S. 1991. Depth distribution of *Calanus finmarchicus* and *C. glacialis* in relation to environmental conditions in the Barents Sea. *Polar Research*, 10: 409–420.
- Wassmann, P., Reigstad, M., Haug, T., Rudels, B., Carroll, M. L., Hop, H., Gabrielsen, G. W. *et al.* 2006. Food webs and carbon flux in the Barents Sea. *Progress in Oceanography*, 71: 232–287.
- Weydmann, A., Carstensen, J., Goszczko, I., Dmoch, K., Olszewska, A., and Kwasniewski, S. 2014. Shift towards the dominance of boreal species in the Arctic: inter-annual and spatial zooplankton variability in the West Spitsbergen Current. *Marine Ecology Progress Series*, 501: 41–52.
- Wiebe, P. H., and Benfield, M. C. 2003. From the Hensen net toward four-dimensional biological oceanography. *Progress in Oceanography*, 56: 7–136.
- Wood, S. N. 2017. mgcv: Mixed GAM Computation Vehicle with GCV/AIC/REML Smoothness Estimation. <https://cran.r-project.org/web/packages/mgcv/index.html>.

*Handling editor: David Fields*