



Original Article

Environmental effects on *Calanus finmarchicus* abundance and depth distribution in the Barents Sea

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The vertical migrations performed by zooplankton at daily and seasonal scales are important for marine ecosystem dynamics and biogeochemical cycles. We analysed associations between seasonal variation in abundance and depth distribution of the copepod *Calanus finmarchicus* and temperature and predation pressure from visual (capelin and herring) and non-visual (ctenophores) predators, using data from a > 30-year survey in the southwestern Barents Sea. *Calanus finmarchicus* abundances were significantly reduced in upper waters with increased capelin biomass, possibly due to a combination of predation mortality and active avoidance of the upper layer. The weighted mean depth of *Calanus finmarchicus* tended to become shallower, and abundances in deeper layers lower, with a high probability of ctenophore occurrence, possibly due to a predation effect at depth. Temperature influenced the seasonal timing of *Calanus finmarchicus*, but appeared less important for depth distribution. This study illustrates how climate-driven changes in the physical and biological environment can influence the seasonal and vertical distribution of zooplankton, which has major implications for the flow of energy and nutrients in marine ecosystems.

Keywords: Barents Sea, *Calanus finmarchicus*, copepod, depth distribution, predation, seasonality, temperature effects, vertical migrations, zooplankton

Introduction

Zooplankton are aquatic animals that spend their lives in the pelagic zone and drift with currents. However, zooplankton are not merely passive drifters. The copepod *Calanus finmarchicus*, the dominant mesozooplankton in the North Atlantic Ocean and adjacent subarctic shelf seas, performs large-scale vertical migrations on diel and seasonal scales (Kashkin, 1962; Melle *et al.*, 2014). Such vertical migrations are important for the food availability for predators, which may modify their behaviour in response to the prey's vertical movement (Hays, 2003; Baumgartner *et al.*, 2011); the drift of zooplankton with ocean currents (Johnson and Checkley, 2004; Johnson *et*

al., 2006); and the transport and recycling of nutrients (Steinberg *et al.*, 2002). In fact, the transport of carbon into the deep sea by seasonally migrating *Calanus finmarchicus* has been estimated to equal the contribution of passively sinking organic material to deep-sea carbon sequestration (Jónasdóttir *et al.*, 2015, 2019).

Simply speaking, diel vertical migration (DVM) is the descent to deeper waters at daytime to avoid visual predators and ascent to the food-rich upper layer at night-time when predation risk is lower, but DVM is a dynamic trait that varies within populations (Mauchline, 1998). Across its distributional range, *Calanus finmarchicus* displays varying degrees of DVM (Manteifel, 1941; Durbin *et al.*, 1995; Dale and Kaartvedt, 2000), with some studies suggesting no

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DVM (Falkenhaug *et al.*, 1997; Basedow *et al.*, 2010). For example, considerable variability in DVM behaviour was observed in the Gulf of Maine, with some copepods in the late copepodite stages (CIV–CV) migrating from the surface to ~100 m at daytime, possibly in response to predation risk from fish, while others remained in surface waters to continue feeding (Baumgartner *et al.*, 2011).

Seasonal vertical migrations are similarly considered a strategy to avoid periodically unfavourable abiotic and biotic conditions (Conover, 1988; Baumgartner and Tarrant, 2017). Late copepodite stages of *Calanus finmarchicus* migrate to depths ranging from several hundred meters to >2000 m in ocean basins, or to shallower depths at the shelves, to diapause (Hirche 1996, Heath 2000, Head & Pepin 2007, Krumhansl *et al.* 2018). The timing and duration of diapause vary regionally, but the onset is typically in late summer or early fall in the northeast Atlantic (Melle *et al.*, 2014).

Timing of seasonal vertical migrations is likely a response to seasonality in environmental conditions (Varpe, 2012). Still, links between environmental drivers such as food availability and temperature, and the timing of diapause in *Calanus finmarchicus*, remain elusive (Johnson *et al.*, 2008; Varpe and Ejsmond, 2018), and predation risk has been proposed as a driver behind seasonal descent (Kaartvedt, 2000; Ji, 2011). Seasonal descent may essentially be a response to a feeding and predation risk trade-off, so that copepods descend when the predation risk in upper waters increase in summer and accumulated lipid reserves are sufficient to sustain diapause (Kaartvedt, 1996; Schmid *et al.*, 2018). Reaching sufficient lipid stores might be the proximate cause that triggers diapause (Maps *et al.*, 2012), but the decision to prepare for diapause instead of producing a new generation is likely triggered by an external cue (Ji, 2011).

Calanus copepods comprise ~80% of the mesozooplankton biomass in the Barents Sea, with *Calanus finmarchicus* dominating in the Atlantic waters in the southwest (Aarflot *et al.*, 2017). *Calanus finmarchicus* typically has a one-year life cycle in this area (Melle and Skjoldal, 1998; Aarflot *et al.*, 2017). Production of a second generation may occur in warm years and become more common with ocean warming (Skaret *et al.*, 2014; Aarflot *et al.*, 2017). Adult females (CVIf) spawn in the upper waters during the phytoplankton spring bloom, and the new generation develops through six nauplii stages (NI – NVI) and five copepodite stages (CI–CV) through spring and summer (Melle and Skjoldal, 1998). Adult males (CVIm) are rarely observed during this period. From around July and onward, mainly stage CV (but also CIV and CVI) descend for overwintering (Kashkin, 1962; Tande *et al.*, 2000). In addition to local production (Dalpadado *et al.*, 2012; Kvile *et al.*, 2017), transport of *Calanus finmarchicus* from the Norwegian Sea is important for maintaining the Barents Sea population (Skaret *et al.*, 2014).

Calanus finmarchicus is an important prey for the main planktivorous fish in the Barents Sea, capelin (*Mallotus villosus*), which has the potential to control zooplankton biomass in parts of the Barents Sea when fish biomass is high (Hassel *et al.*, 1991; Stige *et al.*, 2014). Norwegian spring-spawning herring (*Clupea harengus*) is the other main planktivorous fish in the region. Herring larvae drift from the Norwegian Sea into the southwestern Barents Sea, and juvenile herring remain in the area, predominantly feeding on *Calanus finmarchicus*, before returning to the Norwegian Sea at age 3 or older (Huse and Toresen, 1996; Prokopchuk, 2009, 2019). Considering the strong structuring effect of predation risk on zooplankton vertical distribution (Hays, 2003), it is conceivable that capelin or herring can influence the vertical distribution of *Calanus finmarchicus* in the Barents Sea.

Carnivorous zooplankton may also exert strong predation pressure on *Calanus* populations (Eiane *et al.*, 2002; Ohman *et al.*, 2008). An early study reported reduced *Calanus finmarchicus* biomass in Barents Sea areas with high ctenophore biomass in summer (Manteifel, 1941), which was hypothesized to be due to high copepod mortality. As non-visual predators, gelatinous zooplankton do not depend on light in the upper waters for hunting. Still, the vertical distribution of invertebrate predators may influence the vertical migrations of copepods (Ohman *et al.*, 1983). Temperature may also influence timing of seasonal vertical migrations, for example, it was reported that *Calanus finmarchicus* descended earlier for overwintering in the Barents Sea in warm years (Manteifel, 1941).

To shed light on drivers of *Calanus finmarchicus* vertical distribution, we statistically analysed survey data collected in the southwestern Barents Sea from 1959 to 1992. Aggregated data on total zooplankton biomass in the upper 50 m from the same survey were analysed by Stige *et al.* (2009) and Stige *et al.* (2014). They found that zooplankton biomass tended to be lower in years with high capelin biomass, but higher in the western Barents Sea in years with high herring biomass (Stige *et al.*, 2009), and that zooplankton biomass in spring was positively related to temperature (Stige *et al.*, 2014). Temperature effects on *Calanus finmarchicus* in the upper 50 m from the same dataset were also described by Kvile *et al.* (2014), who found that abundances of the new generation (CI–CIV) peaked earlier with higher temperatures, likely due to earlier spawning and/or faster development. Here, we describe for the first time using these long-term survey data how *Calanus finmarchicus* depth distribution and abundances across depth layers from spring to summer relate to interannual variation in temperature and predation risk. Specifically, we hypothesized that in years with high temperature or predation risk, *Calanus finmarchicus* individuals in the diapausing stages (CIV and CV) would descend earlier to diapause, leading to a reduction of abundances in the upper water layer and a corresponding increase in deeper water layers.

Materials and methods

Zooplankton data

We analysed stage-specific abundances (ind. m⁻³) of *Calanus finmarchicus* copepodite stages (CI–CV) and adults (CVI female and male, hereafter CVIf and CVIm) collected by the Knipovich Polar Research Institute of Marine Fisheries and Oceanography (currently the Polar Branch of Russian Federal Research Institute of Fisheries and Oceanography, VNIRO) (Nesterova, 1990; Kvile *et al.*, 2014). Samples were collected during bi-annual surveys in spring (April–May) and summer (June–July) from 1959 to 1992, using a vertical Juday plankton net with a closing mechanism (37 cm diameter opening, 180- μ m mesh size). There was no survey in the spring of 1967, and no stage-specific data were available from 1980 (summer), 1990 (spring and summer), and 1991 (spring).

The surveys covered the north-eastern Norwegian Sea and southwestern Barents Sea, but we here focus on data from the Barents Sea, i.e. the area between the North Cape–Bear Island transect and the Kola transect (Figure 1). This area is dominated by relatively warm (>3°) and saline (>35) Atlantic waters and colder (>2°) and fresher (<34.7) Coastal waters close to the coast, and remains ice-free year-round (Ingvaldsen and Loeng, 2009). The Atlantic waters are typically vertically mixed down to 200–300 m in winter, and a weak pycnocline is established at <20 m in April–May (Ingvaldsen and Loeng, 2009). The pycnocline is typically strengthened in June,

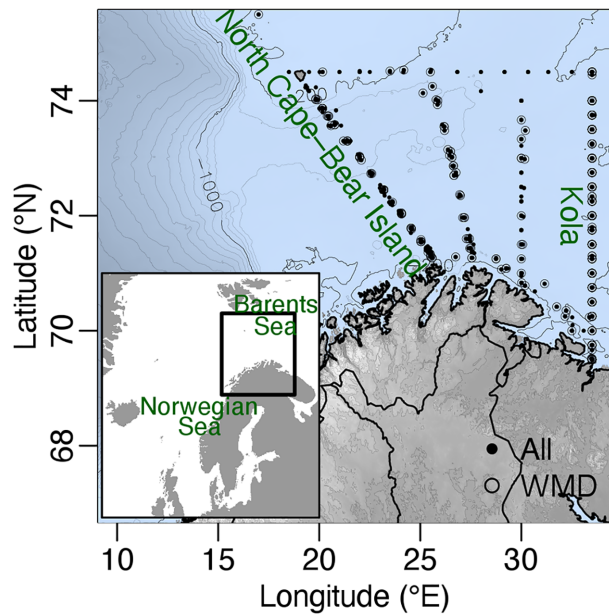


Figure 1. Location of the study area in the southwestern Barents Sea. The detailed map shows the bathymetry (200 m depth contours) and distribution of zooplankton sampling stations, pooled for all years and spring and summer. Small black dots: all sampling stations ($n = 1595$); dots with surrounding circles: sampling stations with coverage of minimum two depth layers (allowing us to calculate weighted mean depth, WMD, $n = 458$).

coinciding with a stronger salinity gradient, and in July–August, it can deepen to ~ 50 m coinciding with a stronger thermocline.

Samples were usually collected from 0 to 50, 50 to 100, and 100 m to the sea floor. Since some sampling depths deviated from this, we classified samples into depth layers using the following criteria (Kvile *et al.*, 2014): Upper layer: upper sampling depth ≤ 20 m and lower sampling depth ≤ 60 m ($n = 1570$); middle layer: upper sampling depth 40–60 m and lower sampling depth ≤ 120 m ($n = 465$); lower layer: upper sampling depth > 90 m ($n = 472$). To obtain information on bottom depth at the stations, we used bathymetry data from the NOAA database with 1-minute grid resolution (Amante and Eakins, 2009).

At stations with minimum two depth layers sampled including the upper layer ($n = 458$), we estimated the weighted mean depth (WMD, m) per stage as in Kvile *et al.* (2019):

$$\text{WMD}_j = \sum_{i=1}^k \frac{\Delta Z_i n_i Z_{m,i}}{N_j} \quad (1)$$

Here, k is the total number of samples (i.e. depth layers) at station j , ΔZ_i is the depth interval (m) of sample i , n_i is the abundance (ind. m^{-3}) of the stage in question in sample i , $Z_{m,i}$ is the mean depth (m) of sample i , and N_j is the depth integrated abundance (ind. m^{-2}) of the stage in question at the station.

Environmental data

We investigated associations between *Calanus finmarchicus* abundance and WMD and the following variables: capelin biomass, juvenile herring biomass, ctenophore occurrence and temperature (Figure 2). We obtained annual estimates of total capelin biomass in the Barents Sea (million tons) based on acoustic surveys in September–October from 1973 to 1993 and cod stomach analyses

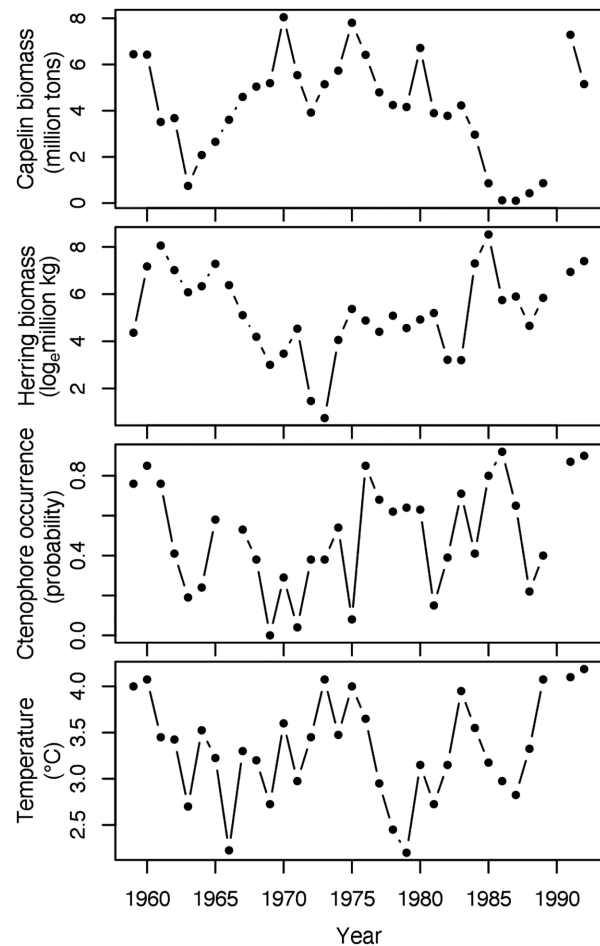


Figure 2. Annual environmental indices included in the statistical analyses: Capelin biomass (million tons), juvenile herring biomass (\log_{10} million kg), mean probability of ctenophore occurrence in summer and mean temperature ($^{\circ}\text{C}$) along the Kola transect from April to July.

before 1973 from Marshall *et al.* (2000), who showed that these two metrics were significantly positively correlated. We calculated a juvenile herring index (hereafter herring biomass) from abundance and weight at age data for Norwegian Spring Spawning Herring (ICES, 2007), summed for ages 1 and 2 and log-transformed to reduce skewness (\log_{10} million kg). We used a semi-quantitative annual index of ctenophores occurrence (mean probability of presence), estimated from bycatch data in fish larvae surveys in summer in the Barents Sea (N. A. Yaragina, L. C. Stige and Ø. Langanen, unpublished data). These data are records of «comb jellies», but the following species were also qualitatively recorded during the surveys and are common in the Barents Sea: *Pleurobrachia pileus*, *Mertensia ovum*, *Bolinopsis infundibulum* and *Beroe cucumis*. Lastly, we calculated an annual temperature index for spring and summer by averaging monthly mean temperature ($^{\circ}\text{C}$) from April to July measured along the Kola transect ($70^{\circ}30' - 72^{\circ}30' \text{N}$, $33^{\circ}30' \text{E}$, 0–200 m depth). None of the environmental indices was significantly correlated (Supplementary material: Table S1).

Statistical analyses

We analysed associations between the environmental variables and *Calanus finmarchicus* abundances and WMD by fitting generalized

additive models (GAM) using the mgcv library (version 1.8–16, Wood 2011) in R (version 3.3.2, R Core Team 2020).

We constructed null models to describe general patterns in stage and depth layer specific abundances and stage-specific WMD. First, to compare spatiotemporal patterns in abundances between depth layers, we fitted the following model to data from one depth layer at the time (upper, middle or lower):

$$\begin{aligned} \text{Abundance null model : } Z = & \beta + s(\text{DOY}) + \text{te}(\text{LON}, \text{LAT}) \\ & + s(\text{BOT}) + s(\text{TIME}) + \varepsilon. \end{aligned} \quad (2)$$

Here, Z is the abundance (ind. m^{-3}) of the stage in question; β is the intercept; $s(\text{DOY})$ is a smooth function of day-of-year with maximally 5 knots (i.e. 4 degrees of freedom); $\text{te}(\text{LON}, \text{LAT})$ is a two-dimensional tensor product of smooth functions of longitude and latitude with maximally 4 knots for each basis function; $s(\text{BOT})$ is a smooth function of bottom depth at the station with maximally 4 knots; $s(\text{TIME})$ is a cyclic smooth function of time of day (continuous numeral between 0 and 24) with maximally 4 knots; and ε is the error term. Since the data were continuous but contained zeroes, we fitted models using the Tweedie distribution with log link (Tweedie, 1984). This distribution handles zeroes and positive values uniformly, and was formulated by setting “family = tw(,)” which log-transforms positive values and estimates the power parameter p during fitting (Wood, 2017).

General spatiotemporal patterns in WMD per stage were described as:

$$\begin{aligned} \text{WMD null model : } -\ln(\text{WMD}) = & \beta + s(\text{DOY}) + \text{te}(\text{LON}, \text{LAT}) \\ & + s(\text{BOT}) + s(\text{Zsum}) + \varepsilon. \end{aligned} \quad (3)$$

Here, WMD is stage-specific WMD that in the statistical analyses was log-transformed to approximate a normal distribution and thereafter converted into negative values. β , $s(\text{DOY})$, $\text{te}(\text{LON}, \text{LAT})$, and $s(\text{BOT})$ correspond to the equivalent terms in the abundance null model, and $s(\text{Zsum})$ is a smooth function of the natural log-transformed total abundances of *Calanus finmarchicus* summed across stages CI–CVI and depth layers (ind. m^{-2} , with maximally 4 knots). Zsum was included to account for potential density dependency in the depth distribution. We also tested to include time of day in the model, but this was never found to be significant. Since the WMD estimates were continuous values, we fitted Equation 3 using a Gaussian distribution.

To describe environmental effects on seasonal variation in depth distribution, we added an interaction term between day-of-year and the indices of capelin biomass, herring biomass, ctenophore occurrence or temperature to the null models. Specifically, we fitted varying coefficient models (Hastie and Tibshirani, 1993) where the effect of the environmental variable was assumed to be linear at any day-of-year, but the slope of the term could vary smoothly with day-of-year (4 knots):

$$\begin{aligned} Z = & \beta + s(\text{DOY}) + s(\text{DOY}) \times \text{ENV} + \text{te}(\text{LON}, \text{LAT}) \\ & + s(\text{BOT}) + s(\text{TIME}) + \varepsilon. \end{aligned} \quad (4)$$

Here, ENV is the environmental variable and the terms $s(\text{DOY}) + s(\text{DOY}) \times \text{ENV}$ together show the seasonal pattern in abundance dependent on the value of ENV for that year. Note that this analysis shows how the average seasonal pattern differs between years, and that responses to local-scale environmental conditions may be stronger than the estimated seasonal pattern. We also considered

environmental models with WMD as response:

$$\begin{aligned} -\ln(\text{WMD}) = & \beta + s(\text{DOY}) + s(\text{DOY}) \times \text{ENV} \\ & + \text{te}(\text{LON}, \text{LAT}) + s(\text{BOT}) + s(\text{Zsum}) + \varepsilon. \end{aligned} \quad (5)$$

To avoid overfitting, we only considered models with one environmental variable at a time, assumed long-term stationarity (the linear effect of the environmental variables can vary with day of year but not between years) and did not consider models with nonlinear effects of environmental variables varying with day of year.

The models including environmental effects were compared to the corresponding null-model using genuine cross-validation (GCV, Ciannelli *et al.*, 2004), a measure of predictive power accounting for spatiotemporal autocorrelation, and deviance explained, a measure of the proportion of data variation explained by the model. GCV was calculated by (i) leaving data from 1 year out at a time, (ii) refitting the model with the reduced data set, (iii) calculating model predictions for the 1 year, and (iv) calculating mean squared prediction errors across all years based on differences in observations and predictions on the $\log_e(N + 1)$ scale. 95% confidence intervals of model effects were computed using nonparametric bootstrapping (1000 samples with replacement) with year as the sampling unit (see Kvile *et al.* 2014).

Results

Calanus finmarchicus abundances in the upper waters in spring–summer were highest for early copepodites (CI–CII) and lowest for adults (CVI, Figure 3a). Abundances decreased with depth, with the strongest reduction in early copepodites. CIV was the most abundant stage in the lower layer (Figure 3c). WMD deepened with copepodite stage (Figure 3d).

Calanus finmarchicus abundances varied significantly with day-of-year, except for CVI in the upper layer and CVIm in the lower layer (Figure 4). Abundances of CI–CV peaked progressively later in the upper layer, from the beginning of June for CI to the end of July or later for CV. Seasonal trends in abundances in the middle and lower layers generally reflected the upper layer, but with higher uncertainty in the patterns. For CIV–CV, there were indications of an increase in abundances in the lower layer at the end of the survey period. Abundances of adults varied less than other stages with day-of-year.

All terms in the Abundance null model (Equation 2) are visualized in Figure S1 (Supplementary material). In short, increased sea floor depth was significantly positively associated with abundances of CI–CII and CVI in the upper layer, and CIII–CIV and CVIm in the lower layer. The effect of time-of-day on abundance was significant for CI—indicating increased abundances in the middle layer in the middle of the day; CIV—indicating reduced abundances in the upper layer in the middle of the day; and CVI—indicating increased abundances in the middle layer from 23:00 to 11:30. Sampling position was significantly associated with abundances for most stages and depth layers (Supplementary material: Figure S1).

WMD tended to be deeper in May and shallower in July in CI–CII (Figure 5). A deepening of WMD in July was indicated for CIV, CV, and CVI, but the association was only significant for CIV. WMD generally deepened with increased sea floor depth. Higher total abundance of *Calanus finmarchicus* was associated with

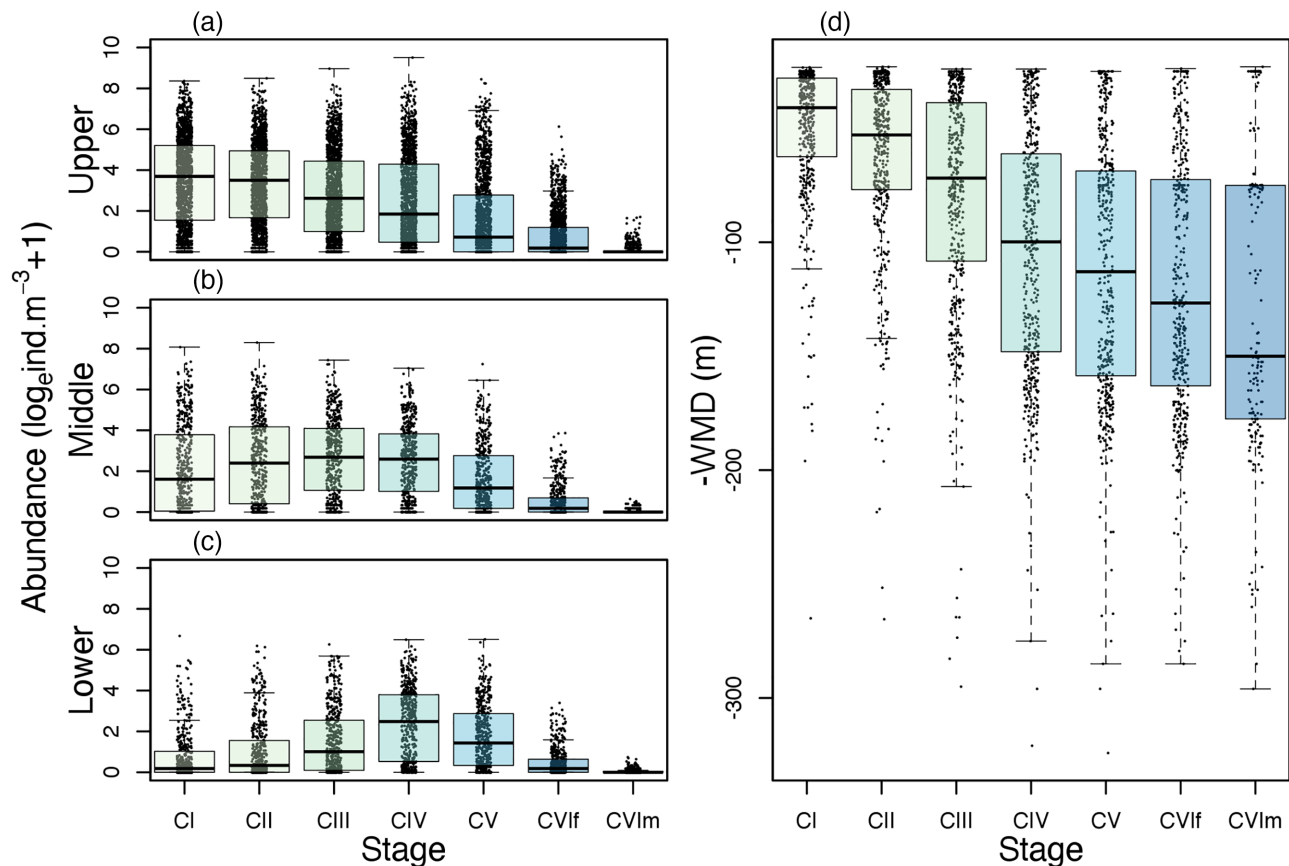


Figure 3. *Calanus finmarchicus* stage-specific abundances per depth layer (a–c) and WMD per stage (d). Observations (points) are shown with overlain boxplot of the median (line), the interquartile range (box) and $1.5 \times$ the interquartile range (whiskers) of the data. To ease visualization, stage-specific abundances (a–c) were natural-log transformed and added a constant of 1.

shallower WMD in CI–CV (statistically significant in CII–CIV, Figure 5). Shallow WMD of CVIf coincided with low total abundances. Finally, WMD of stages CII and older tended to be deeper to the east in the Barents Sea.

Associations between environmental variables and abundances

Our analyses of environmental associations covered seven developmental stages, four environmental variables and abundances in three depth layers plus WMD, resulting in 112 statistical tests and thereby a high risk of false positives. We therefore focus on associations that were consistent across several stages and less on associations that were significant for single stages, as we expect some associations to arise by chance. At the 5% level, we would expect 5–6 false positives among 112 tests. We identified 49 significant associations, including 13 for capelin biomass alone (Figures 6–7, Supplementary material: Figures S2–S3), suggesting that we can have confidence in the main patterns in our results.

Associations between environmental variables and *Calanus finmarchicus* abundances were generally uncertain for the middle and lower layers, and we therefore focus on results for the upper layer, where we have more data. Results for the middle and lower layers are provided in the Supplementary material (Figures S2–S3). Abundances of all stages except CI were significantly reduced in the upper layer with increased capelin biomass (Figure 6a). Abundances

of CII–CIII were predicted to decrease from the end of June, while abundances of CV and CVIf, which were most strongly associated with capelin biomass, were predicted to decrease from early May to early July. For these stages, abundances in the middle layer were also predicted to decrease under high capelin biomass, with a significant effect in early July, while there were no significant associations in the lower layer (Supplementary material: Figures S2–S3).

The only significant associations between herring biomass and *Calanus finmarchicus* abundances in the upper layer were positive associations in May and/or July for CIV–CV (Figure 6b). There were periodically negative associations in the middle and lower layers, e.g. in May for CI–CIII and in July for CIII and CVIf (Supplementary material: Figures S2–S3).

Probability of ctenophore occurrence was in general positively associated to *Calanus finmarchicus* abundances in the upper layer, but the association was only significant for CV and CVIm in mid-May (Figure 6c). Abundance of stages CI–CV in the middle and lower layers tended to be lower in summer with higher probability of ctenophore occurrence, and associations were often stronger than in the upper layer (Supplementary material: Figures S2–S3).

The temperature in spring–summer was positively associated to abundances of stages CI–CIV in the upper layer before June, which for CI–CIII transitioned into a negative association in June–July (Figure 6d). Associations with temperature did not differ much with depth, but were often non-significant in the middle and lower layers (Supplementary material: Figures S2–S3).

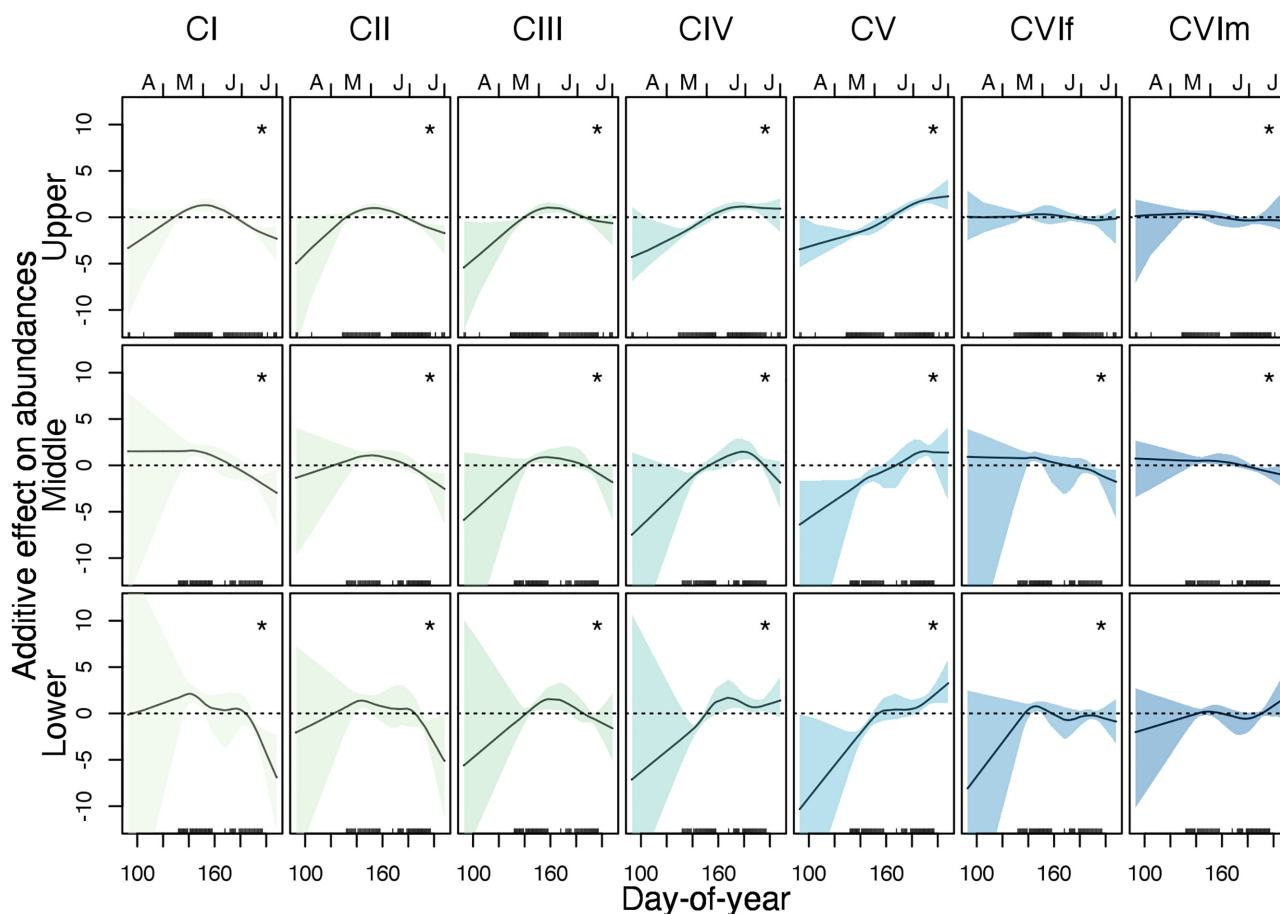


Figure 4. Additive effect of day-of-year on *Calanus finmarchicus* stage-specific abundances ($\log_e \text{ ind.m}^{-3}$, Equation 2), with the model fitted for the upper, middle, and lower water layer, respectively. Asterisks show significant effects, i.e. model terms with p -values < 0.05 and bootstrapped 95% confidence intervals (shaded areas) that exclude 0 (dashed line) in parts of the covariate's range. The rug along the x-axis indicates the location of observations. The upper axis indicates month from April to July.

Associations between environmental variables and WMD

WMD tended to deepen with higher capelin biomass, and was significantly negatively associated with capelin biomass in late June and onward for CII–CIII, and from early June and onward for CIV–CV (Figure 7a). Predicting WMD on the 15th of June under minimum and maximum capelin biomass, setting other model terms to their mean values, indicated that WMD of stages CIV–CV deepened from around 40–60 m to around 130–200 m. WMD was significantly positively associated with herring biomass (shallower WMD) in the beginning and end of the survey for CII and in early July for CIII–CV (Figure 7b).

High probability of ctenophore occurrence was associated with periodically shallower WMD for CII and CIII, and deeper WMD for CVIf (results for CIV, CV and CVIm resembled CIVf but were non-significant, Figure 7c). Finally, WMD tended to be deeper in June with higher temperature, but the association was only significant for CVIf (Figure 7d).

Model comparison

We compared models including an interaction effect between day-of-year and the environmental indices with the null model for each stage, focusing on models fitted for the upper water layer for abun-

dances. In combination, the deviance explained and GCV scores indicated that including a temperature effect improved the abundance models for stages CI–CIII, while adding an effect of capelin biomass improved model fit for stages CIV–CVI (Table 1). There were no consistent effects of environmental indices on WMD; for example, including an effect of ctenophore occurrence resulted in lowest GCV for stages CII–CIV and CVIf, but for CIII and CIV, deviance explained was higher in the herring or capelin model, respectively.

Results for the abundance models fitted for the middle and lower layers indicated that the model with ctenophore occurrence performed best for CII–CIII in both layers, while for CIV, the model with temperature gave the best fit (Supplementary material: Table S2). The model with capelin biomass performed best for adult stages in the middle layer. For other stages, values of deviance explained and GCV were often not in accordance.

Discussion

In this study, we revisited a historical dataset of *Calanus finmarchicus* abundances collected from 1959 to 1992 in the southwestern Barents Sea, and assessed associations between the species' depth distribution and indices representing inter-annual variation in temperature and predation pressure from visual (capelin and herring)

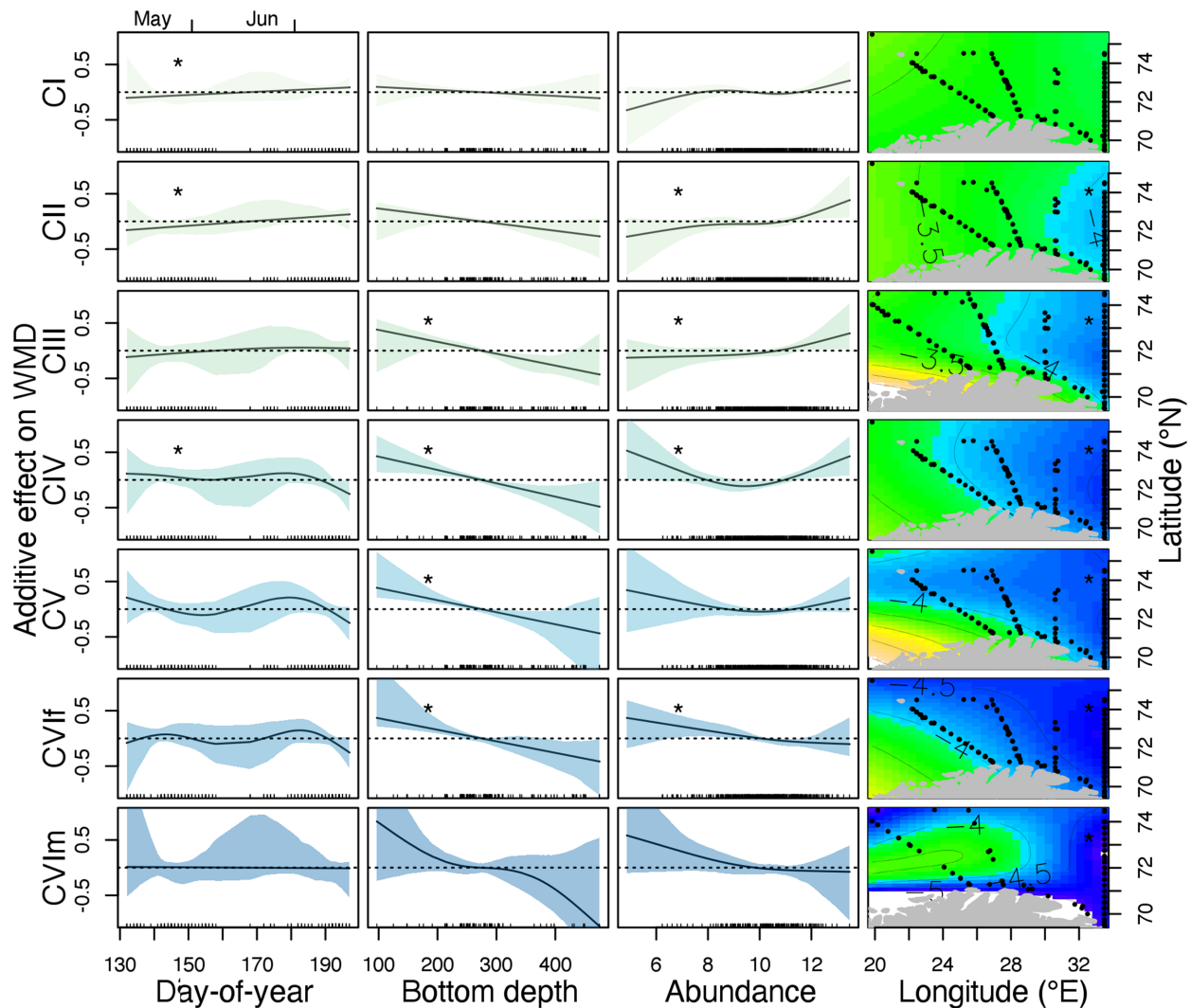


Figure 5. Effects of day-of-year, bottom depth (m), total *Calanus finmarchicus* abundances ($\log_e \text{ ind.m}^{-2}$) and location on stage-specific WMD ($-\log_e \text{ m}$, Equation 3). Negative effect corresponds to deeper WMD. The effect of longitude and latitude is visualized by mapping predicted WMD ($-\log_e \text{ m}$) with other variables set to their mean value (blue = deeper, orange = shallower). Asterisks show significant effects, i.e. model terms with p -values < 0.05 and bootstrapped 95% confidence intervals (shaded areas) that exclude 0 (dashed line) in parts of the covariate's range. The rug along the x-axis (or black dots for the effect of location) indicates the location of observations.

and non-visual (ctenophores) predators. The survey data showed that early copepodites were most abundant in the upper layer, which is expected and in accordance with previous studies as these are actively feeding (non-diapausing) stages (Dale and Kaartvedt, 2000; Daase *et al.*, 2008). Later stages had a deeper and more dispersed vertical distribution. Descent for diapause could explain a deeper distribution of later stages, and the spread in depth may be due the presence of both active and diapausing individuals (Falkenhaus *et al.*, 1997; Daase *et al.*, 2016). Additionally, asynchronous vertical migration in the active population could result in a dispersed vertical distribution (Pearre, 1979; Cottier *et al.*, 2006). There is conflicting evidence of DVM in *Calanus* in the Barents Sea (Basedow *et al.*, 2010; Aarflot *et al.*, 2019). The present data were not sampled to infer diel patterns (stations were sampled once per cruise) and the coarseness of the depth layers limit our ability to detect small-scale vertical migrations (e.g. on the scale of 20–40 m as shown in Daase *et al.* 2016). Still, we found indications of a reduction in the upper

layer during daytime (and in some cases concurrent increases in the middle and/or deeper layers) which appeared to be stronger in later stages (Supplementary material: Figure S1), in line with the expectation of increased DVM amplitude with increased size (Ohman and Romagnan, 2016). Generally, later and larger copepodite stages should be at higher risk of visual predation, which could also explain the deeper distribution in these stages (Dale and Kaartvedt, 2000; Daase *et al.*, 2008).

Associations with predators

Large populations of capelin and herring periodically use the southwestern Barents Sea as feeding ground, with *Calanus finmarchicus* being an important prey (Gjøsæter, 1998; Prokopchuk, 2009, 2019; Orlova *et al.*, 2010). Predation risk from visual predators is highest in the upper waters, and planktivorous fish can periodically graze down copepod biomass in the upper 100 m (Hassel *et*

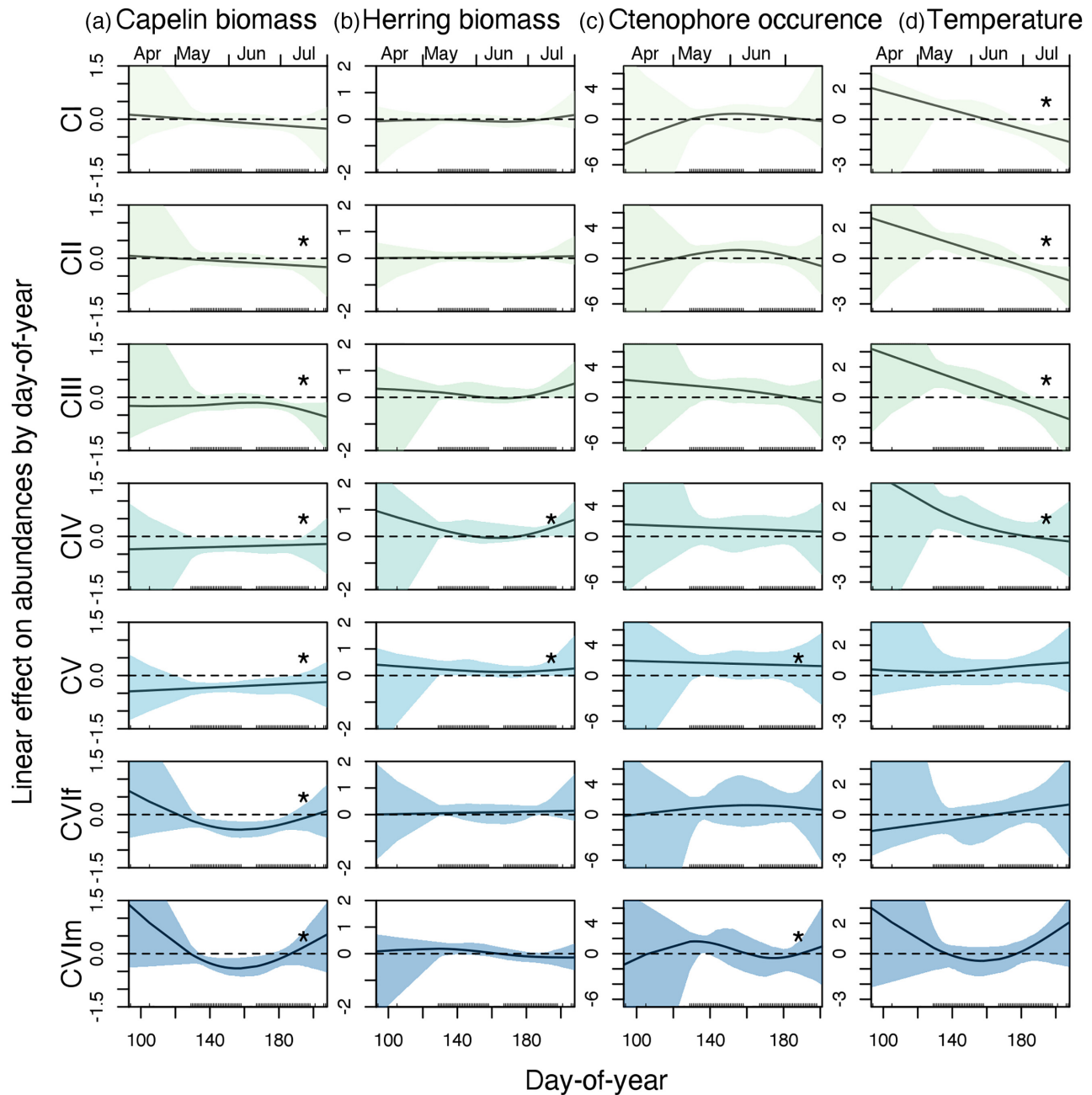


Figure 6. Slope coefficient of the linear effect of environmental variables on *Calanus finmarchicus* stage-specific abundances ($\log_e \text{ ind. m}^{-3}$) per day-of-year in the upper layer. The slope coefficient is the estimated \log_e -scale change in abundance per unit change in the predictor variable (a: capelin biomass = million tons; b: herring biomass = \log_e million kg; c: ctenophore occurrence = probability; d: temperature = $^{\circ}\text{C}$). Asterisks show significant effects, i.e. model terms with p -values < 0.05 and bootstrapped 95% confidence intervals (shaded areas) that exclude 0 (dashed line) in parts of the covariate's range. The rug along the x-axis indicates the location of observations. The y-axis differs between the variables.

al., 1991). We hypothesized that in addition to direct consumption, predation risk could influence *Calanus finmarchicus* depth distribution through vertical migrations. Indeed, abundances in the upper layer tended to be lower—and WMD deeper—under high capelin biomass (Figures 6 and 7). However, while abundances of stages CII–CIII, and CIV–CV in spring, tended to increase in the lower layer under high capelin biomass, the associations were not statistically significantly (Supplementary material: Figure S3), which could

have been expected if predation risk triggered descent. Possibly, our results reflect direct consumption by capelin, as suggested by Stige *et al.* (2009) who analysed data from the same survey and found that total zooplankton biomass in the upper layer was reduced in years with high capelin biomass. Capelin targets larger copepods (Hassel *et al.*, 1991; Orlova *et al.*, 2010), which likely explains why we find a stronger reduction in upper layer abundances for late compared to early copepodite stages (Figure 6) and improvement of the

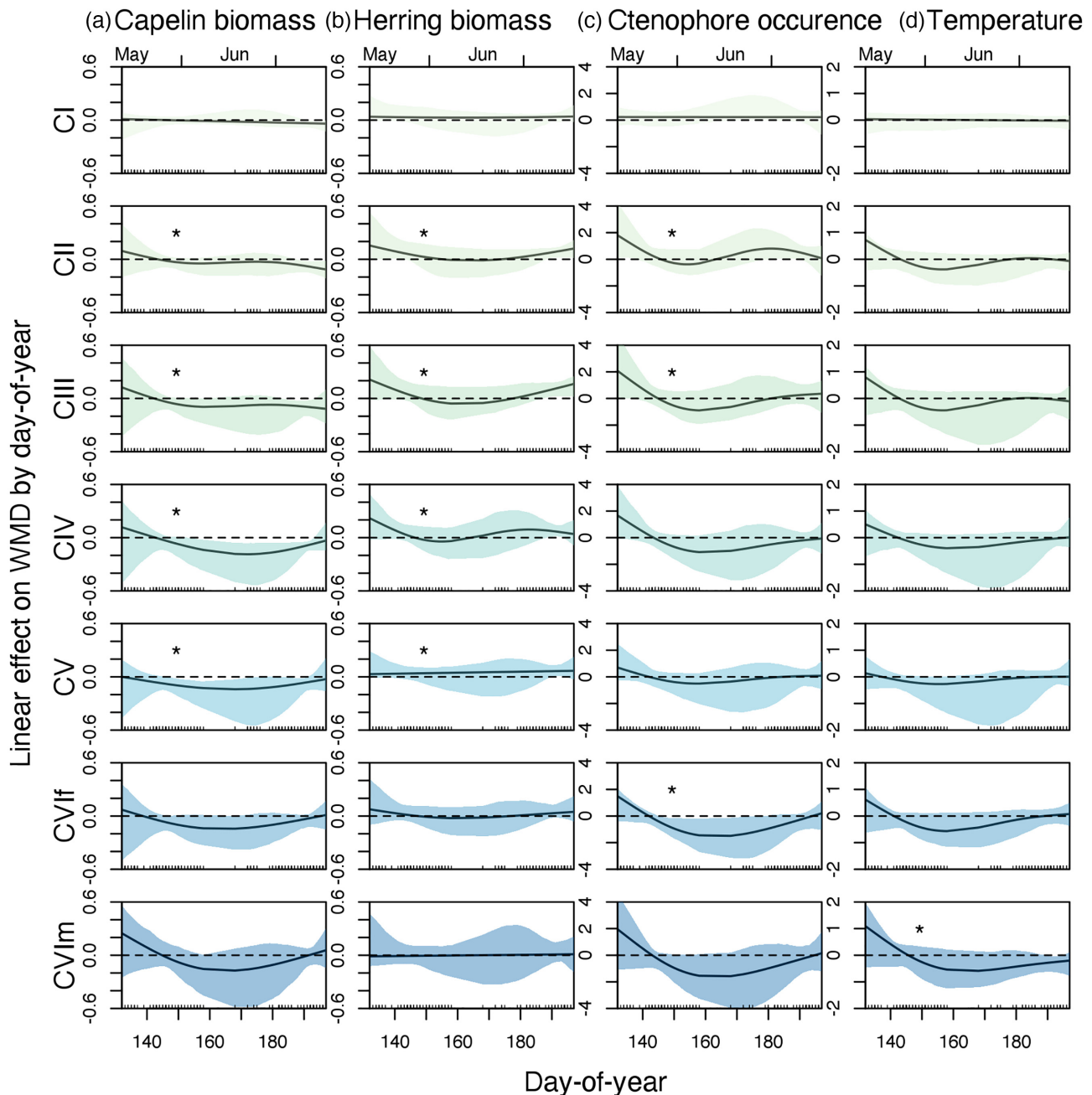


Figure 7. Slope coefficient of the linear effect of environmental variables on stage-specific WMD per day-of-year. The slope coefficient is the estimated change in WMD ($-\log_e$ m) per unit change in the predictor variable (a: capelin biomass = million tons; b: herring biomass = \log_e million kg; c: ctenophore occurrence = probability; d: temperature = $^{\circ}\text{C}$). Negative effect corresponds to deeper WMD. Asterisks show significant effects, i.e. model terms with p -values < 0.05 and bootstrapped 95% confidence intervals (shaded areas) that exclude 0 (dashed line) in parts of the covariate's range. The rug along the x-axis indicates the location of observations. The y-axis differs between the variables.

abundance model with the addition of capelin for stages CIV–CVI (Table 1).

On the other hand, due to the continuous movement between layers, a consistent reduction exclusively in the upper layer appears unlikely unless accompanied by avoidance of the upper layer. *Calanus finmarchicus* can perform DVM spanning from the surface to at least 100 m (Baumgartner *et al.*, 2011; Häfker *et al.*, 2017). The importance of DVM during periods of midnight sun is debated (Blachowiak-Samolyk *et al.*, 2006), but studies at com-

parable latitudes suggest at least small-scale vertical migrations in summer (Dale and Kaartvedt, 2000). Assuming that vertical migrations occur faster than the rate of passive horizontal fluxes through the study system, we would expect losses from mortality in the upper layer to be counteracted by influx of individuals from lower layers, or lead to parallel reductions in the connected deeper layers. We did not find indications of reductions in the lower layer. Note that the reduced data availability from the middle and lower layers could obscure significant patterns, and that the

Table 1. Deviance explained and genuine cross-validation (GCV) for null models and models including interaction effects between day-of-year and environmental variables on *Calanus finmarchicus* abundances ($\log_e \text{ ind.m}^{-3}$) or WMD ($-\log_e \text{ m}$). The highest deviance explained and lowest GCV scores per stage are bolded.

| | | Deviance explained | | | | | GCV | | | | |
|-----------|------|--------------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|
| | | Null | Capelin | Herring | Ctenophores | Temperature | Null | Capelin | Herring | Ctenophores | Temperature |
| Abundance | CI | 0.20 | 0.21 | 0.20 | 0.20 | 0.23 | 5.94 | 5.96 | 5.97 | 6.08 | 5.58 |
| | CII | 0.13 | 0.15 | 0.14 | 0.15 | 0.18 | 5.78 | 5.79 | 5.80 | 5.85 | 5.38 |
| | CIII | 0.09 | 0.13 | 0.11 | 0.11 | 0.13 | 7.10 | 6.67 | 6.89 | 7.05 | 6.64 |
| | CIV | 0.24 | 0.29 | 0.26 | 0.26 | 0.26 | 6.91 | 6.15 | 6.58 | 6.89 | 6.87 |
| | CV | 0.37 | 0.42 | 0.38 | 0.38 | 0.38 | 5.40 | 4.84 | 5.12 | 5.32 | 5.42 |
| | CVlf | 0.17 | 0.25 | 0.17 | 0.18 | 0.17 | 1.55 | 1.39 | 1.58 | 1.59 | 1.60 |
| | CVlm | 0.22 | 0.27 | 0.24 | 0.25 | 0.24 | 0.03 | 0.03 | 0.03 | 0.03 | 0.03 |
| WMD | CI | 0.05 | 0.06 | 0.07 | 0.06 | 0.05 | 0.25 | 0.27 | 0.26 | 0.26 | 0.26 |
| | CII | 0.11 | 0.16 | 0.19 | 0.20 | 0.15 | 0.33 | 0.34 | 0.32 | 0.30 | 0.36 |
| | CIII | 0.14 | 0.20 | 0.24 | 0.22 | 0.18 | 0.39 | 0.42 | 0.37 | 0.35 | 0.46 |
| | CIV | 0.22 | 0.29 | 0.27 | 0.27 | 0.24 | 0.36 | 0.38 | 0.34 | 0.33 | 0.42 |
| | CV | 0.21 | 0.26 | 0.24 | 0.23 | 0.23 | 0.34 | 0.35 | 0.34 | 0.35 | 0.38 |
| | CVlf | 0.20 | 0.24 | 0.21 | 0.25 | 0.23 | 0.35 | 0.38 | 0.37 | 0.32 | 0.37 |
| | CVlm | 0.27 | 0.32 | 0.27 | 0.30 | 0.31 | 0.52 | 0.56 | 0.55 | 0.52 | 0.51 |

For the abundance models, results are shown for the upper water layer. Results for the middle and lower layers are included in Table S2 (Supplementary material).

lower layer did not always cover the water column down to the sea floor.

Basedow *et al.* (2010) observed that *Calanus finmarchicus* were found deeper when their abundance was low, which was explained as avoidance of the upper layer when *per capita* predation risk was high. We did not find clear evidence for density-dependent descent in later stages, however, WMD tended to be shallower in several stages when total abundances of *Calanus finmarchicus* were high. CI–CIII also tended to be present at shallower depths in summer than spring. We may speculate that this relates to increased abundances of older stages, i.e. the early stages are more likely to enter the brighter surface layers when total abundances are high enough to satiate or confuse visual predators. Alternatively, it may relate to the strengthening of the pycnocline in summer (Ingvaldsen & Loeng 2009), which could make it harder for small copepodites such as CI–CII to cross the pycnocline and move below the upper 50-m layer.

Deepening of the WMD in later copepodite stages with high capelin biomass occurred from early June (Figure 7). This matches the timing of capelin feeding in the area (Huse and Toresen, 1996), but is early compared to the timing of the seasonal vertical migration from July onward (Kashkin, 1962; Tande *et al.*, 2000), although there may be considerable interannual and spatial variation in timing of descent. We therefore hypothesize that our results reflect a combination of direct consumption and avoidance of the upper water column by active individuals, or earlier descent for overwintering under high capelin biomass.

We did not find consistent links between herring biomass and *Calanus finmarchicus* abundances or WMD. There were indications of shallower WMD with high herring biomass in some stages, suggesting higher predation at depth, which seems unlikely for a visual predator. Juvenile herring (ages 1–2) are found in the upper 50 m in summer in the Barents Sea, while older herring are distributed deeper (Huse and Toresen, 1996). Stige *et al.* (2009) also found a positive association between zooplankton biomass in the upper 50 m and 1–2-year-old herring, analysing data from the same survey. They proposed that this was driven by a negative associa-

tion between herring and capelin densities (the capelin and herring indices in our study were non-significantly negatively correlated; $r = -0.29$, $p = 0.26$), which could be driven by competition for food (Huse and Toresen, 1996) or predation by herring on capelin larvae (Hjermann *et al.*, 2007). They also highlighted that herring biomass was historically low during the survey period, and that herring therefore may have had a weak feeding effect on zooplankton (Stige *et al.*, 2009).

In general, analyses of predator-prey covariation do not reveal whether relationships are due to predation or to mutual or opposite associations with other drivers (“reciprocal oscillations,” Frank and Leggett, 1985). Increased inflow of Atlantic water from the Norwegian Sea is linked to higher influx of *Calanus finmarchicus* and to wider distribution and improved growth conditions for herring in the Barents Sea (Stenevik and Sundby, 2007). Therefore, mutual associations with Atlantic water masses could explain the positive association between herring biomass and upper-water abundances of some *Calanus finmarchicus* stages. Strong negative correlations between capelin biomass and zooplankton fluctuations in the Barents Sea suggest the presence of a predation effect (Dalpadado *et al.*, 2012, 2020; Stige *et al.*, 2014), which is supported by the dominance of *Calanus* copepods—in addition to euphausiids—in the diet of capelin (Hassel *et al.*, 1991; Orlova *et al.*, 2010). Nonetheless, we cannot exclude the influence of other variables.

We know relatively little about the role of ctenophores in arctic and subarctic ecosystems, but they are highly abundant and may have a significant predatory impact in patches and depth layers with high ctenophore density (Purcell *et al.*, 2010; Majaneva *et al.*, 2013). We found a positive association between *Calanus finmarchicus* abundances in the upper layer and probability of ctenophore occurrence, and a negative association in the middle and lower layers. This may suggest higher predation pressure from ctenophores at depth. We lack data on depth distribution of ctenophores in the study area, and studies from other areas indicate highest abundance in the upper waters in summer (Falkenhaus, 1996; Purcell *et al.*, 2010), but also below 100 m during ctenophores’ abundance peaks in August–September (Bandara *et al.*, 2016). The positive associa-

tion in the upper layer could alternatively be due to a bottom-up effect of copepod abundances on ctenophores. However, since the negative associations in the deeper layers were stronger and more often statistically significant and improving the models than in the upper layer (Supplementary material: Figures S2–S3, Table S2), a top-down effect by ctenophores seems more likely.

Associations with temperature

Temperature influences *Calanus finmarchicus*' growth and development rates (Campbell *et al.*, 2001), timing of spawning (Ellertsen *et al.*, 1987), egg production (Hirche *et al.*, 1997), and mortality rates (Hirst and Kiørboe, 2002). Moreover, mesozooplankton biomass development in the Barents Sea follows the phytoplankton spring bloom with ~1 month's lag (Dalpadado *et al.*, 2020), and since the open-water spring bloom is established by thermo-cline formation, we may expect earlier zooplankton timing with ocean warming. However, no significant trends in phytoplankton spring bloom timing have been detected during recent warming of open-water areas in the Barents Sea (Dalpadado *et al.*, 2020). We hypothesized that temperature could also influence the vertical distribution of *Calanus finmarchicus* through avoidance of the upper, warmer waters or earlier descent for overwintering in warm years (Mantel, 1941; Mauchline, 1998).

Kvile *et al.* (2014) described associations between *Calanus finmarchicus* abundance and temperature using the same dataset as in this study but focusing on the upper water layer. Results indicated that warmer conditions lead to earlier peak of copepodites CI–CIV, which we hypothesized was due to earlier egg production and/or faster development (Kvile *et al.*, 2014). This is supported by the present study, where the model including a temperature effect best explained variation in CI–CIII (Table 1) and suggested that higher temperatures lead to increased abundances of the new generation (CI–CIV) in spring but decreased abundances in summer (Figure 6). Similar patterns were found in the Western Spitzbergen Current, where *Calanus finmarchicus* reached copepodite stage CV earlier during warm years (Weydmann *et al.*, 2018). Although not the focus of the previous study, Kvile *et al.* (2014) pointed out that patterns were consistent across depth, indicating that temperature influences seasonal timing rather than depth distribution. Here, we corroborated this by investigating associations between temperature and WMD, which were largely non-significant (Figure 7). In summary, temperature seems to influence abundances—likely due to an effect on seasonal timing—rather than depth distribution of *Calanus finmarchicus* in the southwestern Barents Sea in spring and summer. Note however that small-scale changes in depth distribution, for example, driven by small-scale variation in thermocline-induced subsurface chlorophyll maxima (Harris, 1988), would not be detected due to the coarse depth strata.

Our statistical approach assumed stationary relationships with environmental variables over years, but if the temperature association operates through different mechanisms that vary in importance over time, this assumption is invalid. Interannual variation in the relationships between *Calanus finmarchicus* and environmental variables has been shown on both sides of the North Atlantic (Hare and Kane, 2012; Hinder *et al.*, 2014), implying that zooplankton–environment linkages must be considered in a historical context and are not necessarily applicable to future conditions. Similarly, interannual variation in fish distribution in our study area or in the relative importance of species captured by the ctenophore index could lead to nonstationary associations. The lack of agreement

between GCV and deviance explained in the model selection for WMD could possibly result from a relatively consistent effect of ctenophores across years (low GCV) whereas the capelin effect was often stronger but less consistent between years (high R^2).

Outlook

The dataset used here covered >30 years and alternating warm and cold conditions in the southwestern Barents Sea (Tande *et al.*, 2000), while the past two decades have seen a strong warming trend linked to increased inflow of Atlantic waters and rising temperatures of inflowing and local water masses (Dalpadado *et al.*, 2020). Mesozooplankton biomass in the Barents Sea varies substantially between years, reaching highest values in years with high temperatures and low sea ice coverage (Dalpadado *et al.*, 2014). The ongoing borealization of the Barents Sea favours Atlantic-water species such as *Calanus finmarchicus* (Aarflot *et al.*, 2017) and creates favourable feeding conditions for pelagic fish such as herring and capelin (Dalpadado *et al.*, 2012). Using long-term data to investigate seasonal variation in *Calanus finmarchicus* abundances and depth distribution, this study improves our understanding of how changes in climatic conditions and predation pressure from fish and invertebrates can influence the seasonal and vertical distribution of this key species.

Supplementary data

Supplementary material is available at the ICES/JMS online version of the manuscript.

Data availability

The zooplankton data underlying this article were provided by the Knipovich Polar Research Institute of Marine Fisheries and Oceanography (currently the Polar Branch of Russian Federal Research Institute of Fisheries and Oceanography, VNIRO) by permission.

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References

- Aarflot, J. M., Aksnes, D. L., Opdal, A. F., Skjoldal, H. R., and Fiksen, Ø. 2019. Caught in broad daylight: topographic constraints of zooplankton depth distributions. *Limnology and Oceanography*, 64: 849–859.
- Aarflot, J. M., Skjoldal, H. R., Dalpadado, P., and Skern-Mauritzen, M. 2017. Contribution of *Calanus* species to the mesozooplankton biomass in the Barents Sea. *ICES Journal of Marine Science*, 1–31.
- Amante, C., and Eakins, B. W. 2009. ETOPO1 1 Arc-Minute Global Relief Model: Procedures, Data Sources and Analysis. NOAA Technical Memorandum NESDIS NGDC-24. <http://www.ngdc.noaa.gov/>

- mgg/global/relief/ETOPO1/docs/ETOPO1.pdf (last accessed date 31 March 2021).
- Bandara, K., Varpe, Ø., Søreide, J., Wallenschus, J., Berge, J., and Eiane, K. 2016. Seasonal vertical strategies in a high-Arctic coastal zooplankton community. *Marine Ecology Progress Series*, 555: 49–64.
- Basedow, S., Tande, K., and Stige, L. 2010. Habitat selection by a marine copepod during the productive season in the Subarctic. *Marine Ecology Progress Series*, 416: 165–178.
- Baumgartner, M. F., Lysiak, N. S. J., Schuman, C., Urban-Rich, J., and Wenzel, F. W. 2011. Diel vertical migration behavior of *Calanus finmarchicus* and its influence on right and sei whale occurrence. *Marine Ecology Progress Series*, 423: 167–184.
- Baumgartner, M. F., and Tarrant, A. M. 2017. The physiology and ecology of diapause in marine copepods. *Annual Review of Marine Science*, 9: 387–411.
- Blachowiak-Samolyk, K., Kwasniewski, S., Richardson, K., Dmoch, K., Hansen, E., Hop, H., Falk-Petersen, S. et al. 2006. Arctic zooplankton do not perform diel vertical migration (DVM) during periods of midnight sun. *Marine Ecology Progress Series*, 308: 101–116.
- 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.
- Ciannelli, L., Chan, K., Bailey, K. M., and Stenseth, N. C. 2004. Non-additive effects of the environment on the survival of a large marine fish population. *Ecology*, 85: 3418–3427.
- 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.
- Cottier, F. R., Tarling, G. A., Wold, A., and Falk-Petersen, S. 2006. Unsynchronized and synchronized vertical migration of zooplankton in a high arctic fjord. *Limnology and Oceanography*, 51: 2586–2599.
- Daase, M., Eiane, K., Aksnes, D. L., and Vogedes, D. 2008. Vertical distribution of *Calanus* spp. and *Metridia longa* at four Arctic locations. *Marine Biology Research*, 4: 193–207.
- Daase, M., Hop, H., and Falk-Petersen, S. 2016. Small-scale diel vertical migration of zooplankton in the High Arctic. *Polar Biology*, 39: 1213–1223. Springer, Berlin and Heidelberg.
- Dale, T., and Kaartvedt, S. 2000. Diel patterns in stage-specific vertical migration of *Calanus finmarchicus* in habitats with midnight sun. *ICES Journal of Marine Science*, 57: 1800–1818.
- 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.
- Dalpadado, P., Arrigo, K. R., van Dijken, G. L., Skjoldal, H. R., Bagøien, E., Dolgov, A. V., Prokopchuk, I. P. et al. 2020. Climate effects on temporal and spatial dynamics of phytoplankton and zooplankton in the Barents Sea. *Progress in Oceanography*, 185: 102320.
- Dalpadado, P., Ingvaldsen, R. B., Stige, L. C., Bogstad, B., Knutsen, T., Ottersen, G., and Ellertsen, B. 2012. Climate effects on Barents Sea ecosystem dynamics. *ICES Journal of Marine Science*, 69: 1303–1316.
- Durbin, E. G., Campbell, R. G., Gilman, S. L., and Durbin, A. G. 1995. Diel feeding behavior and ingestion rate in the copepod *Calanus finmarchicus* in the southern Gulf of Maine during late spring. *Continental Shelf Research*, 15: 539–570.
- Eiane, K., Aksnes, D. L., Ohman, M. D., Wood, S., and Martinussen, M. B. 2002. Stage-specific mortality of *Calanus* spp. under different predation regimes. *Limnology and Oceanography*, 47: 636–645.
- Ellertsen, B., Fossum, P., Solemdal, P., Sundby, S., and Tilseth, S. 1987. The effect of biological and physical factors on the survival of Arcto-Norwegian cod and the influence on recruitment variability. In *The effect of oceanographic conditions on distribution and population dynamics of commercial fish in the Barents Sea*. Proceedings of the third Soviet-Norwegian Symposium, Murmansk, 26–28 May 1986, pp. 101–126. Ed. by Loeng, H. Institute of Marine Research, Bergen.
- Falkenhaus, T. 1996. Distributional and seasonal patterns of ctenophores in Malangen, northern Norway. *Marine Ecology Progress Series*, 140: 59–70.
- Falkenhaus, T., Tande, K. S., and Semenova, T. 1997. Diel, seasonal and ontogenetic variations in the vertical distributions of four marine copepods. *Marine Ecology Progress Series*, 149: 105–119.
- Frank, K. T. and Leggett, W. C. 1985. Reciprocal oscillations in densities of larval fish and potential predators: a reflection of present or past predation. *Canadian Journal of Fisheries and Aquatic Sciences*, 42: 1841–1849.
- Gjosæter, H. 1998. The population biology and exploitation of capelin (*Mallotus villosus*) in the Barents sea. *Sarsia*, 83: 453–496.
- Häfker, N. S., Meyer, B., Last, K. S., Pond, D. W., Hüppe, L., and Teschke, M. 2017. Circadian clock involvement in zooplankton diel vertical migration. *Current Biology*, 27: 2194–2201.e3.e3.
- Hare, A. J., and Kane, J. 2012. Zooplankton of the Gulf of Maine—a changing perspective. In *Advancing an Ecosystem Approach in the Gulf of Maine*, pp. 115–137. Ed. by Stephenson, R., Annala, J., Runge, J., and Hall-Arber, M. American Fisheries Society, Bethesda, MD.
- Harris, R. P. 1988. Interactions between diel vertical migratory behavior of marine zooplankton and the subsurface chlorophyll maximum. *Bulletin of Marine Science*, 43: 663–674.
- Hassel, A., Skjoldal, H. R., Gjosæter, 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.
- Hastie, T., and Tibshirani, R. 1993. Varying-coefficient models. *Journal of the Royal Statistical Society*, 55: 757–796.
- Hays, G. C. 2003. A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia*, 503: 163–170.
- Head, E., and Pepin, P. 2007. Variations in overwintering depth distributions of *Calanus finmarchicus* in the slope waters of the NW Atlantic continental shelf and the Labrador Sea. *Journal of Northwest Atlantic Fishery Science*, 39: 49–69.
- Heath, M. 2000. Winter distribution of *Calanus finmarchicus* in the Northeast Atlantic. *ICES Journal of Marine Science*, 57: 1628–1635.
- Hinder, S. L., Gravenor, M. B., Edwards, M., Ostle, C., Bodger, O. G., Lee, P. L. M., Walne, A. W. et al. 2014. Multi-decadal range changes vs. thermal adaptation for north east Atlantic oceanic copepods in the face of climate change. *Global Change Biology*, 20: 140–146.
- Hirche, H.-J. 1996. Diapause in the marine copepod, *Calanus finmarchicus* — A review. *Ophelia*, 44: 129–143.
- Hirche, H.-J., Meyer, U., and Niehoff, B. 1997. Egg production of *Calanus finmarchicus*: effect of temperature, food and season. *Marine Biology*, 127: 609–620.
- Hirst, A., and Kjørboe, T. 2002. Mortality of marine planktonic copepods: global rates and patterns. *Marine Ecology Progress Series*, 230: 195–209.
- Hjermann, D., Bogstad, B., Eikeset, A. M., Ottersen, G., Gjosæter, H., and Stenseth, N. C. 2007. Food web dynamics affect Northeast Arctic cod recruitment. *Proceedings of the Royal Society B: Biological Sciences*, 274: 661–669.
- Huse, G., and Toresen, R. 1996. A comparative study of the feeding habits of herring (*Clupea harengus*, Clupeidae, L.) and capelin (*Mallotus villosus*, Osmeridae, Müller) in the Barents Sea. *Sarsia*, 81: 143–153.
- ICES. 2007. Report of the Working Group on Northern Pelagic and Blue Whiting Fisheries (WGNPBW), 27 August–1 September 2007, Vigo. *ICES CM 2007/ACFM:29*. www.ices.dk.
- Ingvaldsen, R. B., and Loeng, H. 2009. Physical oceanography. In *Ecosystem Barents Sea*, pp. 33–64. Ed. by Sakshaug, E., Johnsen, G., and Kovacs, K. Tapir Academic Press, Trondheim.
- Ji, R. 2011. *Calanus finmarchicus* diapause initiation: new view from traditional life history-based model. *Marine Ecology Progress Series*, 440: 105–114.
- Johnson, C. L., and Checkley, D. M. 2004. Vertical distribution of diapausing *Calanus pacificus* (Copepoda) and implications for transport in the California undercurrent. *Progress in Oceanography*, 62: 1–13.
- Johnson, C. L., Leising, A. W., Runge, J. A., Head, E. J. H., Pepin, P., Plourde, S., and Durbin, E. G. 2008. Characteristics of *Calanus fin-*

- marchicus* dormancy patterns in the Northwest Atlantic. ICES Journal of Marine Science, 65: 339–350.
- Johnson, C., Pringle, J., and Chen, C. 2006. Transport and retention of dormant copepods in the Gulf of Maine. Deep Sea Research Part II: Topical Studies in Oceanography, 53: 2520–2536.
- Jónasdóttir, S. H., Visser, A. W., Richardson, K., and Heath, M. R. 2015. Seasonal copepod lipid pump promotes carbon sequestration in the deep North Atlantic. Proceedings of the National Academy of Sciences, 112: 12122–12126.
- Jónasdóttir, S. H., Wilson, R. J., Gislason, A., and Heath, M. R. 2019. Lipid content in overwintering *Calanus finmarchicus* across the Subpolar Eastern North Atlantic Ocean. Limnology and Oceanography, 64: 2029–2043.
- Kaartvedt, S. 1996. Habitat preference during overwintering and timing of seasonal vertical migration of *Calanus finmarchicus*. Ophelia, 44: 145–156.
- Kaartvedt, S. 2000. Life history of *Calanus finmarchicus* in the Norwegian Sea in relation to planktivorous fish. ICES Journal of Marine Science, 57: 1819–1824.
- Kashkin, N. I. 1962. Adaptive significance of seasonal migrations in *Calanus finmarchicus* (Gunnerus, 1770) (Canadian Translation of Fisheries and Aquatic Sciences No. 4869). Zoological Journal, 41: 342–357.
- Krumhansl, K. A., Head, E. J. H., Pepin, P., Plourde, S., Record, N. R., Runge, J. A., and Johnson, C. L. 2018. Environmental drivers of vertical distribution in diapausing *Calanus* copepods in the Northwest Atlantic. Progress in Oceanography, 162: 202–222.
- Kvile, K. Ø., Ashjian, C., and Ji, R. 2019. Pan-Arctic depth distribution of diapausing *Calanus* copepods. The Biological Bulletin, 237: 76–89.
- Kvile, K. Ø., Dalpadado, P., Orlova, E., Stenseth, N. C., and Stige, L. C. 2014. Temperature effects on *Calanus finmarchicus* vary in space, time and between developmental stages. Marine Ecology Progress Series, 517: 85–104.
- Kvile, K. Ø., Fiksen, Ø., 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.
- Majaneva, S., Berge, J., Renaud, P. E., Vader, A., Stübner, E., Rao, A. M., Sparre *et al.* 2013. Aggregations of predators and prey affect predation impact of the Arctic ctenophore *Mertensia ovum*. Marine Ecology Progress Series, 476: 87–100.
- Manteifel, B. P. 1941. Plankton and herring in the Barents Sea. Trudy PINRO. Transactions of the Knipovich Polar Scientific Institute of Sea-Fisheries and Oceanography Murmansk, 7: 125–218 (in Russian).
- Maps, F., Runge, J. A., Leising, A., Pershing, A. J., Record, N. R., Plourde, S., and Pierson, J. J. 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.
- Marshall, C. T., Yaragina, N. a., Ådlandsvik, B., and Dolgov, A. V. 2000. Reconstructing the stock-recruit relationship for Northeast Arctic cod using a bioenergetic index of reproductive potential. Canadian Journal of Fisheries and Aquatic Sciences, 57: 2433–2442.
- Mauchline, J. 1998. Advances In Marine Biology: The biology of calanoid copepods. Academic Press: London. 710pp.
- 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.
- 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.
- Nesterova, V. N. 1990. Plankton biomass along the drift route of cod larvae (reference material). PINRO, Murmansk (in Russian). 64pp.
- Ohman, M. D., Durbin, E. G., Runge, J. A., Sullivan, B. K., and Field, D. B. 2008. Relationship of predation potential to mortality of *Calanus finmarchicus* on Georges Bank, northwest Atlantic. Limnology and Oceanography, 53: 1643–1655.
- Ohman, M. D., Frost, B. W., and Cohen, E. B. 1983. Reverse diel vertical migration: an escape from invertebrate predators. Science, 220: 1404–1407.
- Ohman, M. D., and Romagnan, J.-B. 2016. Nonlinear effects of body size and optical attenuation on Diel Vertical Migration by zooplankton. Limnology and Oceanography, 61: 765–770.
- Orlova, E. L. El, Rudneva, G. G. B., Renaud, P. E. P., Eiane, K., Savinov, V., and Yurko, A. S. A. 2010. Climate impacts on feeding and condition of capelin *Mallotus villosus* in the Barents Sea: evidence and mechanisms from a data set spanning 30 years. Aquatic Biology, 10: 105–118.
- Pearre, S. 1979. Problems of detection and interpretation of vertical migration. Journal of Plankton Research, 1: 29–44.
- Prokopchuk, I. 2009. Feeding of the Norwegian spring spawning herring *Clupea harengus* (Linne) at the different stages of its life cycle. Deep Sea Research Part II: Topical Studies in Oceanography, 56: 2044–2053.
- Prokopchuk, I. 2019. Feeding ecology of immature herring *Clupea harengus* in the Barents Sea. *In* Influence of Ecosystem Changes on Harvestable Resources at High Latitudes. The Proceedings of the 18th Russian-Norwegian Symposium, pp.151–160, Ed. by Shamray, E., Huse, G., Trofimov, A., Sundby, S., Dolgov, A., Skjoldal, H. R., Sokolov, K. *et al.* Murmansk, 5–7 June 2018
- Purcell, J. E., Hopcroft, R. R., Kosobokova, K. N., and Whitledge, T. E. 2010. Distribution, abundance, and predation effects of epipelagic ctenophores and jellyfish in the western Arctic Ocean. Deep Sea Research Part II: Topical Studies in Oceanography, 57: 127–135.
- R Core Team. 2020. R: A language and environment for statistical computing. <http://www.r-project.org/> (last accessed date 31 March 2021).
- Schmid, M. S., Maps, F., and Fortier, L. 2018. Lipid load triggers migration to diapause in Arctic *Calanus* copepods—insights from underwater imaging. Journal of Plankton Research, 40: 311–325.
- Skaret, G., Dalpadado, P., Hjøllø, 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.
- Steinberg, D. K., Goldthwait, S. A., and Hansell, D. A. 2002. Zooplankton vertical migration and the active transport of dissolved organic and inorganic nitrogen in the Sargasso Sea. Deep Sea Research Part I: Oceanographic Research Papers, 49: 1445–1461.
- Stenevik, E. K., and Sundby, S. 2007. Impacts of climate change on commercial fish stocks in Norwegian waters. Marine Policy, 31: 19–31.
- Stige, L. C., Dalpadado, P., Orlova, E., Boulay, A.-C. 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.
- Stige, L. C., Lajus, D. L., Chan, K.-S., Dalpadado, P., Basedow, S., Berchenko, I., and Stenseth, N. C. 2009. Climatic forcing of zooplankton dynamics is stronger during low densities of planktivorous fish. Limnology and Oceanography, 54: 1025–1036.
- Tande, K., Drobysheva, S., Nesterova, V., Nilssen, E. M., Edvardsen, A., and Tereschenko, V. 2000. Patterns in the variations of copepod spring and summer abundance in the northeastern Norwegian Sea and the Barents Sea in cold and warm years during the 1980s and 1990s. ICES Journal of Marine Science, 57: 1581–1591.
- Tweedie, M. C. K. 1984. An index which distinguishes between some important exponential families. *In* Statistics: Applications and New Directions. Proceedings of the Indian Statistical Insti-

- tute Golden Jubilee International Conference, pp. 579–604. Ed. by Ghosh, J. K., and Roy, J. Indian Statistical Institute. Calcutta, India.
- Varpe, Ø. 2012. Fitness and phenology: annual routines and zooplankton adaptations to seasonal cycles. *Journal of Plankton Research*, 34: 267–276.
- Varpe, Ø., and Ejsmond, M. J. 2018. Trade-offs between storage and survival affect diapause timing in capital breeders. *Evolutionary Ecology*, 32: 623–641.
- Weydmann, A., Walczowski, W., Carstensen, J., and Kwaśniewski, S. 2018. Warming of Subarctic waters accelerates development of a key marine zooplankton *Calanus finmarchicus*. *Global Change Biology*, 24: 172–183.
- Wood, S. N. 2017. *Generalized additive models: an introduction with R*. Chapman and Hall/CRC, Boca Raton, FL.
- Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society*. 73: 3–36.

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