

Pan-Arctic Depth Distribution of Diapausing *Calanus* Copepods

KRISTINA ØIE KVILE^{1,2,*}, CARIN ASHJIAN², AND RUBAO JI²

¹Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, P.O. Box 1066 Blindern, 0316 Oslo, Norway; and ²Biology Department, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543

Abstract. Diapause at depth is considered an integral part of the life cycle of *Calanus* copepods, but few studies have focused on the Arctic species *Calanus glacialis* and *Calanus hyperboreus*. By analyzing a large set of pan-arctic observational data compiled from multiple sources, we show that Arctic *Calanus* has a broad depth distribution in winter, indicating that diapause at depth is a facultative strategy. Both species' vertical distributions tend to deepen in winter and to be deeper and broader with increasing bottom depth, while individuals are aggregated closer to the sea floor in shallow areas. These results indicate that Arctic *Calanus* species pursue a relatively deep diapause habitat but are topographically blocked on the shelves. Interspecific differences in depth distribution during diapause suggest the importance of predation. The larger *C. hyperboreus* has a deeper diapause depth than *C. glacialis*, potentially to alleviate predation pressure or as a result of predation loss near the surface. Moreover, the mean depth of *C. hyperboreus* in winter is negatively associated with latitude, indicating a shoaling of the diapause population in the central Arctic Ocean where predation pressure is lower. Our results suggest a complex diapause behavior by Arctic *Calanus*, with implications for our view of the species' roles in Arctic ecosystems.

Introduction

Many organisms respond to periodically unfavorable environmental conditions by entering a state of dormancy. In the abundant marine pelagic copepods in the order Calanoida,

dormancy can take the form of resting eggs or postembryonic diapause, the latter being a state of arrested development typically occurring in late developmental stages (Williams-Howze, 1997; Baumgartner and Tarrant, 2017 and references therein). Postembryonic diapause has been widely studied in the North Atlantic species *Calanus finmarchicus* and is considered an integral part of the life cycle of all *Calanus* species (Conover, 1988). In high-latitude environments such as the Arctic Ocean, strong seasonality in photoperiod, temperature, and resource availability favors dormancy strategies (Dahms, 1995); but research on diapause in the Arctic *Calanus* species is relatively scarce (Baumgartner and Tarrant, 2017).

Calanus glacialis and *Calanus hyperboreus* dominate zooplankton biomass in the Arctic Ocean (Kosobokova and Hopcroft, 2010) and play important roles in the Arctic ecosystem and in the carbon cycle. In preparation for diapause, these copepods accumulate carbon-rich lipid reserves that constitute an important energy source for animals at higher trophic levels, including fish, marine mammals, and birds (Dahl *et al.*, 2003; Falk-Petersen *et al.*, 2009; Davies *et al.*, 2014). By migrating to deep waters, diapausing *Calanus* species efficiently sequester carbon into the deep ocean, a process that can be regionally important for the carbon budget (Jónasdóttir *et al.*, 2015, 2019; Visser *et al.*, 2017). *Calanus glacialis* and *C. hyperboreus* develop from freely spawned eggs through six naupliar stages and five copepodid stages into the adult stage (male or female). Because of its larger size, *C. hyperboreus* can store sufficient lipid for diapause from an earlier stage (C3 is considered its first diapausing stage, while C4 and C5 are the main diapausing stages of *C. glacialis*); therefore, it can spend more years completing its life cycle (depending on the environment, the life span of *C. hyperboreus* ranges from one to five years, compared to one to three years for *C. glacialis*) (Falk-Petersen *et al.*, 2009). And while *C. glacialis* females can use lipid reserves (capital breeding) or feed on ice algae or phytoplankton blooms to fuel egg production (income breeding)

Received 8 February 2019; Accepted 16 May 2019; Published online 17 September 2019.

* To whom correspondence should be addressed. Email: k.o.kvile@ibv.uio.no.

Abbreviations: C1–C5, copepodid stages C1–C5; C6f and C6m, female and male adult stage C6; DVM, diel vertical migration; SD, standard deviation of weighted mean depth; WMD, weighted mean depth.

Online enhancement: supplementary appendix.

(Daase *et al.*, 2013), *C. hyperboreus* is an exclusive capital breeder that reproduces at depth in winter.

Despite the importance of diapausing *Calanus* in the Arctic, logistical challenges limit the number of available observations; and synoptic accounts of the diapause habitats are rare (but see Visser *et al.*, 2017). The diapause habitat of *C. hyperboreus* has been characterized as deep basin areas, including at 500–2000-m depth in the central Arctic Ocean and at 1000–2000 m in the North Atlantic (Vinogradov, 1997), 500–3000 m in the Greenland Sea Gyre (Hirche, 1997), and >1000 m in the Fram Strait/West Spitsbergen Current (Hirche, 1997; Auel *et al.*, 2003) and in the Norwegian Sea (Østvedt, 1955). *Calanus glacialis* has been observed to diapause at shallower depths than *C. hyperboreus*, for example, at around 200–500 m in the western Arctic Ocean (Ashjian *et al.*, 2003) and 200–400 m in the central Arctic basins (Vinogradov, 1997). In the Greenland Sea, diapausing stages of *C. glacialis* were observed from a few hundred meters to 2000 m (Hirche, 1991).

Diapausing at depth has several potential advantages. For example, descending to colder layers can allow copepods to increase the duration of lipid reserves and sustain longer starvation periods by reducing their metabolic rate (Ingvarsdóttir *et al.*, 1999; Saumweber and Durbin, 2006). However, the hypothesis that minimizing metabolism is the main driver behind diapause habitat selection is contradicted by the large variation in temperatures experienced during diapause by *C. finmarchicus* populations (Melle *et al.*, 2014) and observations of diapausing *Calanus* in the relatively warm Atlantic water layer in the Arctic Ocean (Hirche, 1997). Second, increased water density at depth can allow lipid-rich copepods to remain neutrally buoyant, thereby saving energy (Visser and Jónasdóttir, 1999; Pond and Tarling, 2011), although the depth of neutral buoyancy is not temporally stable, and other mechanisms may be needed to remain neutrally buoyant (Campbell and Dower, 2003; Sartoris *et al.*, 2010; Freese *et al.*, 2015). Third, lower ambient light at depth can reduce predation by visual predators (Kaarvedt, 1996), and model results suggest that increased predation pressure together with increased temperature and/or reduced food availability can trigger diapause (Ji, 2011). For example, the *Calanus* community in an Arctic fjord descended while food availability was still high (Bandara *et al.*, 2016), indicating that increased temperature or predation pressure in summer-fall triggered diapause. Importantly, regardless of the environmental conditions, individuals must acquire sufficient lipid reserves before they can diapause, or they must otherwise continue feeding in the upper layer (Schmid *et al.*, 2018).

If upper waters are unfavorable for diapause in terms of temperature, density, predation pressure, or other factors, *Calanus* copepods have likely evolved to seek out diapause habitat below a certain depth threshold where conditions are more favorable. As a result, we expect that on a pan-arctic scale, the mean depth of the diapausing population is positively associated with bottom depth down to a certain depth threshold, where benefits

of descending deeper do not compensate for the migration cost. Similarly, we expect that as the availability of favorable diapause habitat increases with bottom depth, the depth distribution of diapausers will broaden. For example, Krumhansl *et al.* (2018) observed denser near-bottom winter aggregations of *Calanus* on the Canadian Atlantic shelf than in deeper areas, indicating that diapausers seek out depths that are unavailable on the shelf, while optimal diapause habitat is found across a broader depth range in deeper areas (see also Aarflot *et al.*, 2018).

Toward the poles, both temperature gradients with depth and predation pressure by visual predators are lower (Kaarvedt, 2008), potentially reducing the advantage of migrating to great depths and resulting in a shoaling of diapause depth with latitude. This was suggested by Hirche (1991), who

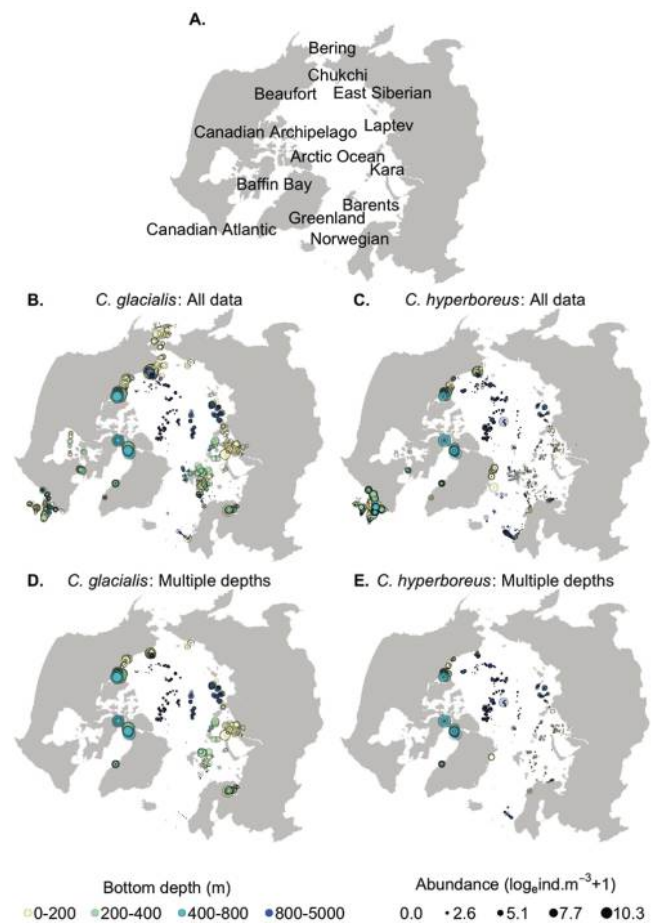


Figure 1. (A) Map of the study area. (B–E) Observed abundances of *Calanus glacialis* (B, D) and *Calanus hyperboreus* (C, E) in winter (natural logarithm of individual [ind.] m⁻³ + 1, summed for all copepodid stages and adults), pooled from all sampling stations (B, C) or stations with at least two sampled depth intervals (D, E). Observations from different depth layers are overlaid (not summed). Circle size and color indicate abundances and bottom depth at the station, respectively.

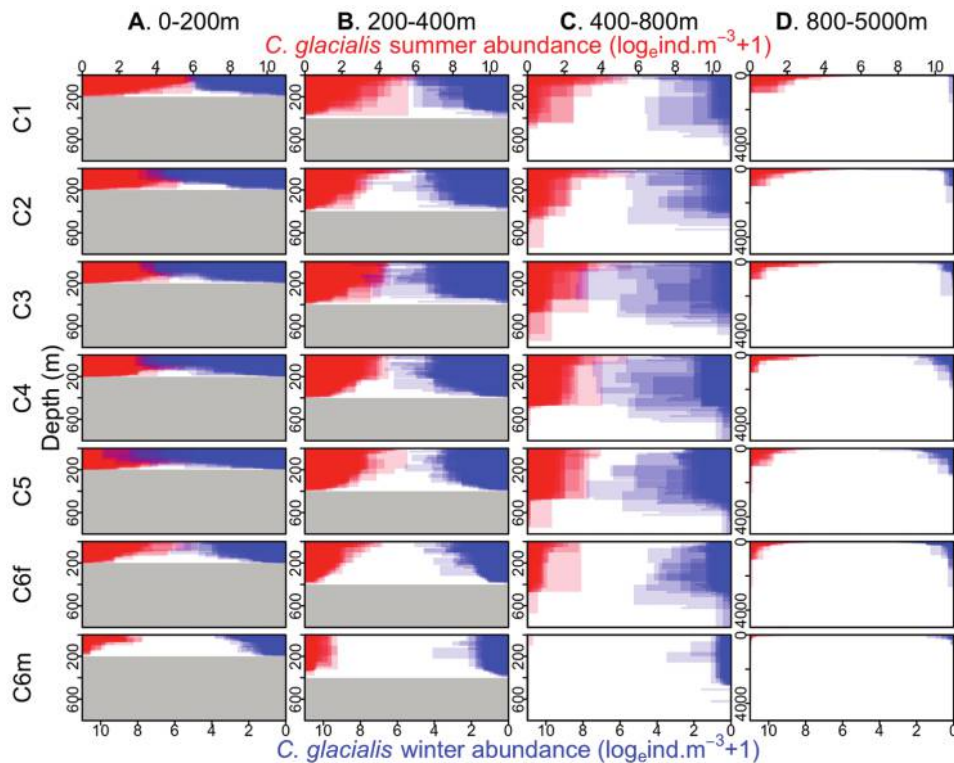


Figure 2. Vertical distribution of *Calanus glacialis* stages for different bottom depth ranges (indicated with gray shading) in summer (red bars, upper x-axis) and winter (blue bars, lower and inverted x-axis), pooled for all available data. Each bar is one observation, with bar length representing observed abundances and bar width the sampled depth interval (darker color indicates a larger number of overlapping observations in depth). To facilitate visualization, data were natural log transformed. Note the different y-axis for 800–5000-m bottom depth. C1–C5, copepodid stages C1–C5; C6f and C6m, female and male adult stage C6.

observed that *C. hyperboreus* occupied deeper winter habitats in the Greenland Sea compared to the central Arctic basins.

In this study, we analyze compiled observational data of Arctic *Calanus*, spanning from the shelves to the deep basins. We aim to describe the diapause habitat of *C. glacialis* and *C. hyperboreus* on a pan-arctic scale and to quantify associations between diapause depth and bottom depth or latitude.

Materials and Methods

Overview of approach

This study is based on a recent compilation of published observational data spanning the Arctic Ocean and surrounding seas from the 1930s to present (Kvile *et al.*, 2018). The dataset contains information on abundances of *Calanus glacialis* Jaschnov, 1955 and *Calanus hyperboreus* Krøyer, 1838 copepodid and adult stages per location, time, and depth interval. Since we lack information about physiology, we cannot determine whether sampled individuals are in “true diapause,” that is, a state of arrested development and reduced metabolism (Maps *et al.*, 2014). Instead, we assume that individuals observed in winter are in diapause.

Although the duration of the winter season varies in space and between years, observations of the seasonal migrations of Arctic *Calanus* are relatively consistent. For example, *C. hyperboreus* has been observed to diapause from around mid-August to April in the Greenland Sea and the Resolute Passage (Conover, 1988; Hirche, 1997), September to April–May in the central Arctic (Dawson, 1978), September to March–May in the Gulf of St. Lawrence (Plourde *et al.*, 2003), and September through March in the western Arctic Ocean (Ashjian *et al.*, 2003) (note that since *C. hyperboreus* spawns at depth in winter, it is difficult to distinguish spawning and diapausing females from vertical distribution alone). Kosobokova and Hirche (2009) similarly stated that the seasonal downward migration of *Calanus*-dominated biomass in the central Arctic starts in September and remains at depth until May–June. Based on most of these observations, we define September through April as winter in this study.

Copepodid stage C3 has been described as the first diapausing stage of *C. glacialis* and *C. hyperboreus*; however, there appears to be great regional variation, and stage C4 is often considered the main diapausing stage of *C. glacialis* (reviewed in Falk-Petersen *et al.*, 2009). Instead of focusing only on later stages, we here analyze data for all copepodid

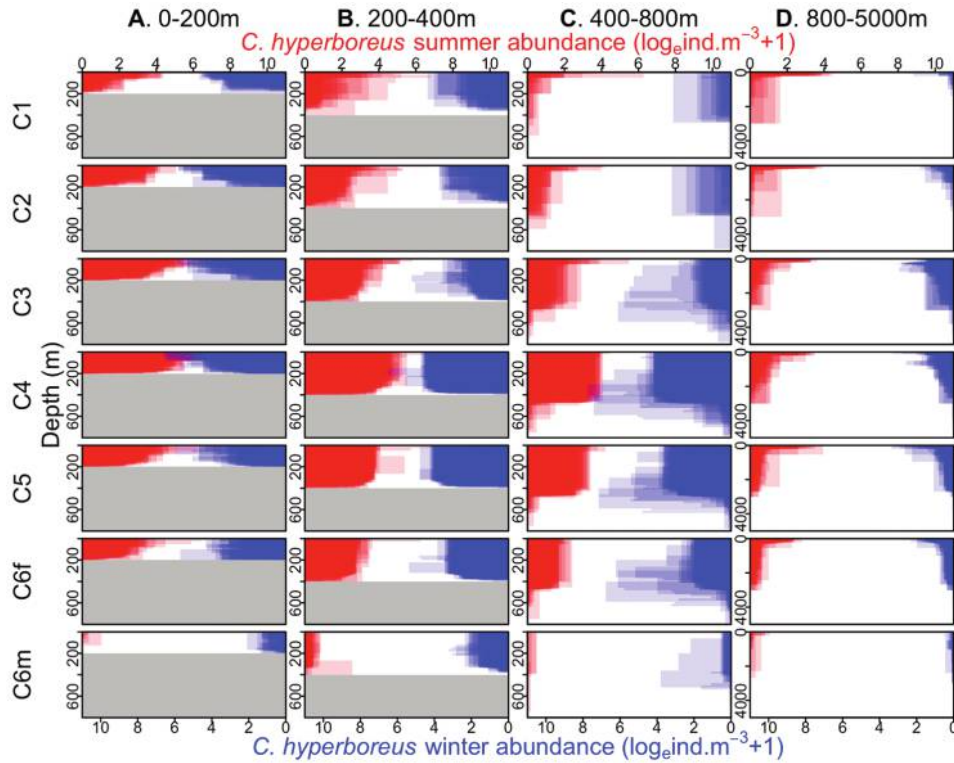


Figure 3. Vertical distribution of *Calanus hyperboreus* stages for different bottom depth ranges (indicated with gray shading) in summer (red bars, upper x-axis) and winter (blue bars, lower and inverted x-axis), pooled for all available data. Each bar is one observation, with bar length representing observed abundances and bar width the sampled depth interval (darker color indicates a larger number of overlapping observations in depth). To facilitate visualization, data were natural log transformed. Note the different y-axis for 800–5000-m bottom depth. C1–C5, copepodid stages C1–C5; C6f and C6m, female and male adult stage C6.

stages and adults. Similarly, instead of using a fixed depth threshold to define diapause, we investigate how the species’ depth distribution varies in space and time.

Data compilation

We compiled observational data on *C. glacialis* and *C. hyperboreus* as described in Kvile *et al.* (2018). In short, we compiled stage-specific abundance data on copepodid stages (C1–C5) and adults (C6 female or male; hereafter, C6f and C6m) from published sources (see Supplementary Table 1, available online). We included only observations of abundances (individual [ind.] m^{-3} or $ind. m^{-2}$) rather than biomass or presence; and we excluded observations pooled across stages or where sampling date, location (longitude and latitude), depth (upper and lower depths of sample), gear, or mesh size was unknown. We focused on depth-specific density data ($ind. m^{-3}$; hereafter referred to as abundances), converting any depth-integrated observations ($ind. m^{-2}$) to $ind. m^{-3}$ by using the sampled depth interval. If observations of the same species and stage in a dataset were a mix of positive and missing values (NAs) without zeros, we assumed that NAs were zeros.

Large mesh size relative to body size can result in underestimation of abundance. Since mesh size differed between datasets, we converted observed abundance ($ind. m^{-3}$) in station i , $N_{caught}(i)$, to expected abundances, $N_{total}(i)$, using the function from Nichols and Thompson (1991):

$$\frac{N_{caught}(i)}{N_{total}(i)} = \frac{1}{1 + e^{-8.9(R-1)}}, \quad (1)$$

where R is the body width:mesh size ratio, using stage-specific body widths (R. G. Campbell [University of Rhode Island], pers. comm.). For both species, this correction had minimal or no influence on stages C4–C6, while for younger stages, observed abundances were corrected (*i.e.*, increased) at mesh sizes more than $\sim 200 \mu m$ (for C1), $\sim 250\text{--}275 \mu m$ (for C2), and $\sim 350 \mu m$ (for C3; see Supplementary Fig. 1, available online), with larger effects for smaller body width : mesh size ratio. We excluded samples where $N_{caught}/N_{total} < 25\%$, since at this level of undersampling the abundance estimates could become highly inflated. This resulted in removal of 11%, 0.17%, and 0.07% of the data for *C. glacialis* C1–C3, respectively, and 10%, 0.17%, and 0.07% of the data for *C. hyperboreus* C1–C3, respectively.

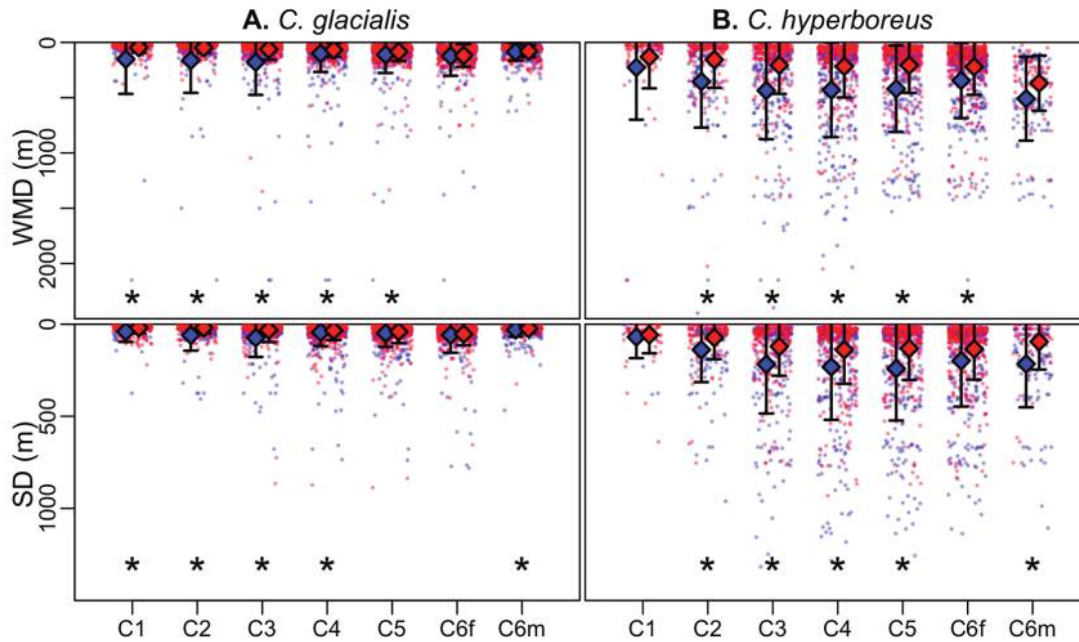


Figure 4. (A) *Calanus glacialis* and (B) *Calanus hyperboreus* weighted mean depth (WMD) and standard deviation of weighted mean depth (SD) in winter (blue) and summer (red). Small circles show stage-specific estimates from individual sampling stations, pooled for all regions. To distinguish individual estimates, random noise was added to the x-axis position. Diamonds and black vertical lines show mean values and standard deviations around the mean. Significant differences between seasons are marked with asterisks ($P < 0.01$). C1–C5, copepodid stages C1–C5; C6f and C6m, female and male adult stage C6.

Quantifying *Calanus* depth distribution

To visualize the spatial distribution of *C. glacialis* and *C. hyperboreus* in winter (September–April), we mapped observations pooled from all datasets and depth intervals. We compared observations between areas with bottom depths of 0–200 m (“shallow shelf”), 200–400 m (“deep shelf”), 400–800 m (“slope”), and >800 m (“basin”). If sea bottom depth was not given in the original dataset, we used the closest depth estimate from the International Bathymetric Chart of the Arctic Ocean (IBCAO ver. 3.0, June 8, 2012, <https://www.ngdc.noaa.gov/mgg/bathymetry/arctic/ibcaoversion3.html>; 500-m spatial resolution) or Southern Alaska Coastal Relief Model (24-arc-second resolution) (Lim *et al.*, 2011).

The large variation in sampled depth intervals in different datasets challenged any synthesis of variation in abundances with depth. We first constructed overlaid bar plots of stage-specific abundances in winter and summer for the four depth regions described above, with the bar width indicating sampled depth interval. To further quantify variation in abundances by depth, we estimated the weighted mean depth (WMD, m) and standard deviation (SD, m) per sampling station and stage as in Aarflot *et al.* (2018):

$$WMD_j = \sum_{i=1}^k \frac{\Delta Z_i n_i Z_{m,i}}{N_j}, \quad (2)$$

$$SD_j = \sqrt{\sum_{i=1}^k \frac{\Delta Z_i n_i Z_{m,i}^2}{N_j} - WMD_j^2}, \quad (3)$$

where 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. To standardize data from stations with variable depth coverage, we calculated average stage-specific abundances (ind. m^{-3}) per 50-m depth bin from the surface to the bottom, and we used the binned averages to calculate WMD and SD. When calculating binned averages, we considered data from any sample with at least 5-m overlap with the bin in question and included only stations with at least 2 sampled layers.

Statistical analyses

Significant differences in WMD and SD were tested using the nonparametric Kruskal-Wallis one-way ANOVA and, subsequently, the two-sided Wilcoxon rank sum test to compare individual stage pairs (results using one-way ANOVA indicated violations of the assumption of normally distributed residuals). To quantify associations between WMD or SD and bottom depth or latitude, we used univariate or multivariate

Table 1

Average weighted mean depth (WMD; m, upper row) and standard deviation of weighted mean depth (SD; m, left column) of *Calanus glacialis* and *Calanus hyperboreus* stages in winter and P-values from a Wilcoxon rank sum test of differences in WMD (above the diagonal) and SD (below the diagonal) between stage pairs

		WMD																
		<i>C. glacialis</i>							<i>C. hyperboreus</i>									
		C1	C2	C3	C4	C5	C6f	C6m	C1	C2	C3	C4	C5	C6f	C6m			
		152	163	180	100	110	123	85	226	354	435	429	419	344	509			
SD	<i>C. glacialis</i>	C1	40	0.82	0.03	0.08	0.79	0.29	0.06	0.71	0.00	0.00	0.00	0.00	0.00	0.00	0.00	C1
		C2	60	0.09		0.04	0.05	0.61	0.38	0.03	0.59	0.00	0.00	0.00	0.00	0.00	0.00	C2
		C3	74	0.01	0.36		0.00	0.00	0.02	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	C3
		C4	44	0.67	0.00	0.00		0.00	0.00	0.29	0.96	0.00	0.00	0.00	0.00	0.00	0.00	C4
		C5	49	0.80	0.01	0.00	0.54		0.00	0.00	0.52	0.00	0.00	0.00	0.00	0.00	0.00	C5
		C6f	58	0.08	0.51	0.06	0.00	0.00		0.00	0.23	0.00	0.00	0.00	0.00	0.00	0.00	C6f
		C6m	31	0.11	0.00	0.00	0.00	0.00	0.00		0.77	0.00	0.00	0.00	0.00	0.00	0.00	C6m
WMD	<i>C. hyperboreus</i>	C1	69	0.88	0.43	0.21	0.66	0.96	0.43	0.32	0.00	0.00	0.00	0.00	0.00	0.00	C1	
		C2	139	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02		0.03	0.05	0.03	0.35	0.00	C2
		C3	218	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01		0.69	0.88	0.04	0.01	C3
		C4	232	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.54		0.74	0.13	0.00	C4
		C5	241	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.28	0.62		0.05	0.00	C5
		C6f	199	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.45	0.11	0.03		0.00	C6f
		C6m	216	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.57	0.82	0.83	0.22		C6m
		C1	C2	C3	C4	C5	C6f	C6m	C1	C2	C3	C4	C5	C6f	C6m			
		<i>C. glacialis</i>							<i>C. hyperboreus</i>									
		SD																

Significant differences ($P < 0.01$) are shown in bold.

linear regression models with WMD or SD in winter as the response variable. To reduce the risk of Type I errors (false positives) when testing multiple associations, we set the significance level to $P < 0.01$.

Results

Spatial distribution in winter

Calanus glacialis and *Calanus hyperboreus* have a pan-arctic distribution in winter (Fig. 1B, C). Both species are abundant in winter in shelf and slope regions of the Baffin Bay, Canadian archipelago, and Beaufort Sea, while only *C. glacialis* is present in the Chukchi and Bering Seas. *Calanus glacialis* is more abundant than *C. hyperboreus* in the eastern Arctic shelf seas (Barents, Kara, and Laptev Seas), while the latter dominates in the Canadian Atlantic (Newfoundland-Labrador Shelf and Gulf of St. Lawrence). Both species are found in winter in the central Arctic basins, where *C. hyperboreus* generally reaches higher abundances than its congener. Selecting stations with a minimum of two sampled depth layers reduces data availability, for example, in the Chukchi and Bering Seas, the Canadian Atlantic, and the Greenland and Barents Seas (Fig. 1D, E).

Variation in depth distribution per depth region

For both species, the compiled data indicate that in summer, the highest depth-specific abundances are found on the shelves (<400-m bottom depth; Figs. 2, 3). Although highest summer abundances typically are observed close to the surface, both species have a broad depth distribution. In winter, abundances remain high on the shelves; but, in contrast to summer, winter abundances increase in the slope regions (400–800-m bottom depth), where average winter abundances are highest for *C. glacialis* C1–C4 and C6f and *C. hyperboreus* C3–C6. While the compiled data suggest a broad depth distribution of both species also in winter, later stages (C3–C6f) appear to peak below ~200 m. High abundances of the early copepodid stages (C1 and C2) of both species are also found throughout the water column in winter. Depth-specific abundances are relatively low in the basins (>800-m bottom depth) and concentrated in the upper ~500 m.

Variation in weighted mean depth and standard deviation

Both species are generally found deeper and more dispersed in winter than in summer (Fig. 4). Specifically, for all stages

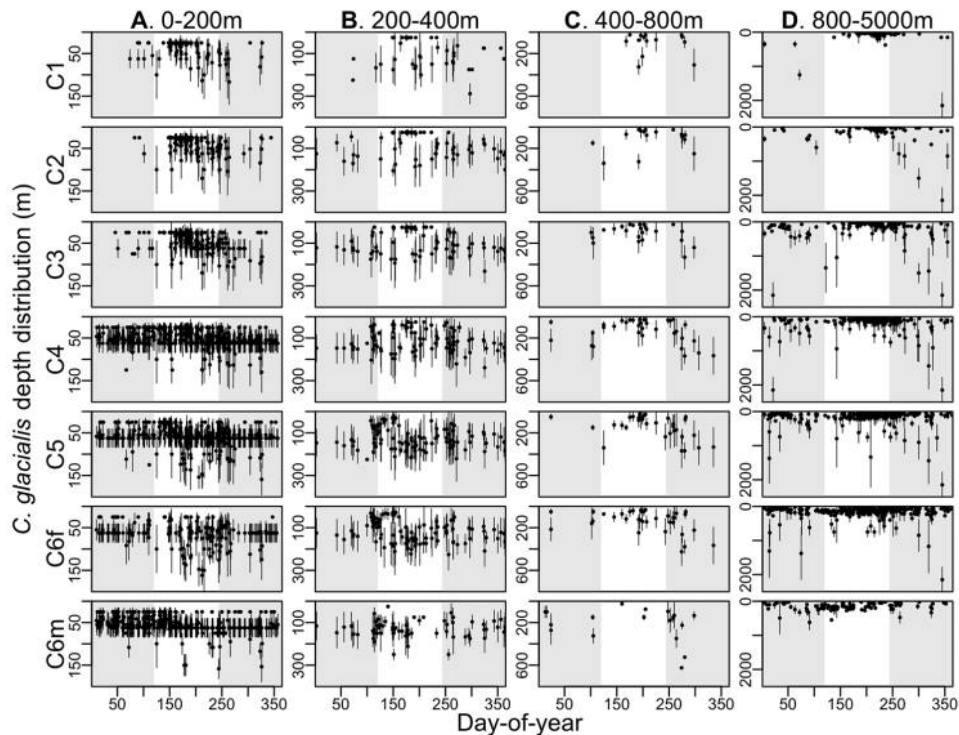


Figure 5. Estimated weighted mean depth (WMD; black filled circles) \pm standard deviation of weighted mean depth (SD; vertical lines) per day of year for *Calanus glacialis* stages in different bottom depth ranges. The winter season is shaded in gray. Note that the y-axes differ between bottom depth ranges. C1–C5, copepodid stages C1–C5; C6f and C6m, female and male adult stage C6.

except *C. glacialis* C6 (f and m) and *C. hyperboreus* C1 and C6m, the WMD is significantly deeper in winter (Wilcoxon rank sum test, $P < 0.01$). The SD is significantly higher in winter for all stages except *C. glacialis* C5 and C6f and *C. hyperboreus* C1 and C6f. Furthermore, *C. hyperboreus* is generally found deeper and more dispersed than *C. glacialis*. In winter, WMD estimates for *C. hyperboreus* C2–C6f do not differ significantly from each other but are significantly deeper than all *C. glacialis* stages (Table 1). Conversely, the WMD of *C. hyperboreus* C1 in winter is significantly shallower than other *C. hyperboreus* stages and resembles *C. glacialis*, while *C. hyperboreus* C6m is found significantly deeper than any other stage. Some *C. glacialis* stages also differ intraspecifically in depth distribution in winter; for example, stage C3 is found significantly deeper than C4, C5, and C6m. The generally deeper distribution of *C. hyperboreus* reflects within-station depth differences, not only different spatial distributions; that is, station-specific differences in WMD calculated for corresponding stages from the two species are significantly different from zero for all stages except C1 and C2.

Similarly, except for stage C1, *C. hyperboreus* is significantly more dispersed in depth (higher SD) in winter than *C. glacialis* (Table 1). Significant intraspecific differences in SD also occur; for example, *C. hyperboreus* C1 and C2 are less dispersed than later stages, and *C. glacialis* C2 and C3 are significantly more dispersed than C4, C5, and C6m (Table 1).

Although it is difficult to identify a clear seasonal migration pattern in the compiled data, our defined winter season corresponds relatively well with a deepening of the Arctic *Calanus* populations, with a clearer difference in areas with bottom depth >400 m (Figs. 5, 6). On the shelf, the seasonal difference is limited; notably, there are many observations of *C. glacialis* in the shallow shelf region (<200 -m bottom depth) with a relatively shallow WMD throughout the year (Fig. 5).

Associations with bottom depth and latitude

Except for stage C1 of both species, there is consistently a significant positive linear relationship ($P < 0.01$) between bottom depth and WMD or SD when fitting univariate linear models, that is, a deeper and broader depth distribution in winter with increased bottom depth (Fig. 7; Table 2). Associations with latitude in the univariate models are a mix between nonsignificant, significantly positive, and significantly negative. Latitude and bottom depth are positively correlated in the compiled dataset (Kendall's rank correlation coefficient, $\tau = 0.45$, $P < 0.01$); therefore, multivariate linear models were fitted to quantify associations with latitude when taking into account the potentially confounding effect of bottom depth. Except for *C. glacialis* C6m, associations with bottom depth remain significant and positive in the multivariate

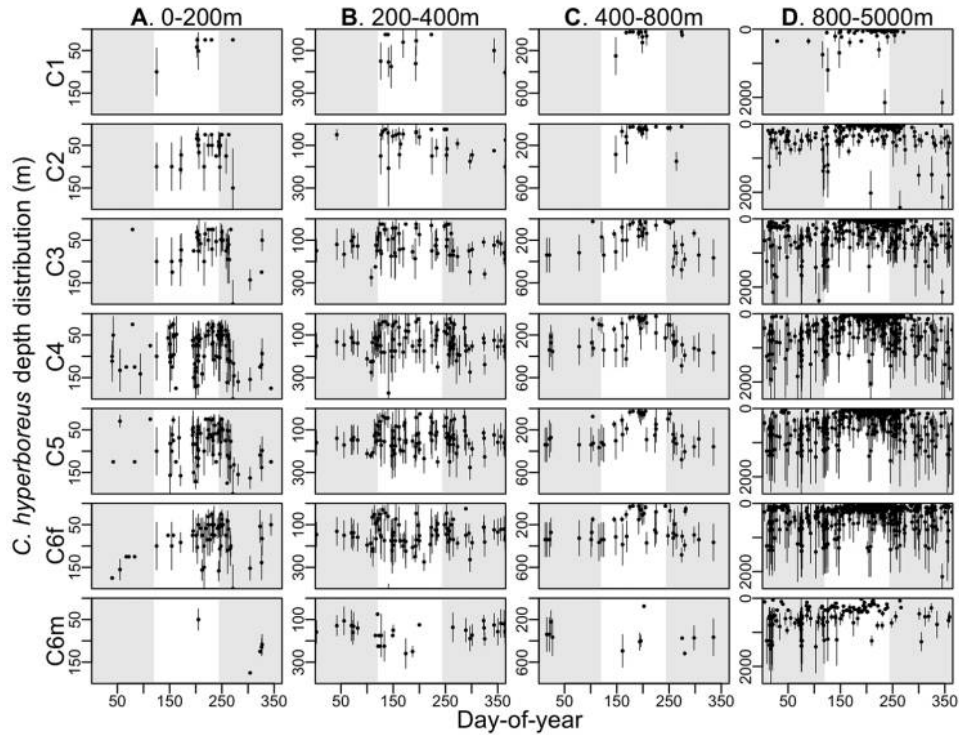


Figure 6. Estimated weighted mean depth (WMD; black filled circles) \pm standard deviation of weighted mean depth (SD; vertical lines) per day of year for *Calanus hyperboreus* stages in different bottom depth ranges. The winter season is shaded in gray. Note that the y-axes differ between bottom depth ranges. C1–C5, copepodid stages C1–C5; C6f and C6m, female and male adult stage C6.

models; in contrast, associations with latitude become mostly negative (Table 2). Significant negative associations with latitude are found for WMD and SD of *C. hyperboreus* C2–C6 (m and f) and *C. glacialis* C6f.

The positive association between bottom depth and WMD and SD could reflect that individuals use the available water column but do not necessarily descend closer to the sea floor. To test this, alternative models were fitted with WMD and SD divided by bottom depth as response variables, representing at which percentage of the water column from the surface WMD is found and the percentage of the water column used, respectively. For both species, these indices are for most stages negatively associated with bottom depth and latitude in both univariate and multivariate models (Fig. 8; Table 3). Relative to the total water column, diapausers tend to be found closer to the bottom, but they also occupy a larger part of the water column at shallower and lower-latitude locations. For most *C. hyperboreus* stages, however, associations between SD and bottom depth are nonsignificant in the multivariate models.

Since our definition of winter (September–April) likely is too broad in many regions covered by the dataset (see *Discussion*), we performed sensitivity analyses using a more re-

strictive definition (October–March). This did not change the main patterns in our results (not shown).

Discussion

Arctic *Calanus* species are typically depicted as herbivorous copepods that take advantage of the short growth season to accumulate lipid reserves to sustain dormancy at depth in winter. However, recent work has shown that the role of omnivory has been underappreciated (*e.g.*, Campbell *et al.*, 2009, 2015). The diapause habitat of *Calanus hyperboreus* is considered to be at >500-m depth in ocean basins, including the Arctic basins, the Amundsen Gulf, the Baffin Sea, and the Icelandic, Norwegian, and Greenland Seas (Falk-Petersen *et al.*, 2009; Visser *et al.*, 2017), while *C. glacialis* is associated with shallower depths (Ashjian *et al.*, 2003). In both species, the diapause population consists of later-stage copepodids capable of storing sufficient lipid (reviewed in Falk-Petersen *et al.*, 2009).

We compiled and analyzed a large set of observational data from studies spanning the Arctic Ocean and surrounding seas from the 1930s to present. In contrast to the classical view of diapausers residing in deep basins in winter, the compiled

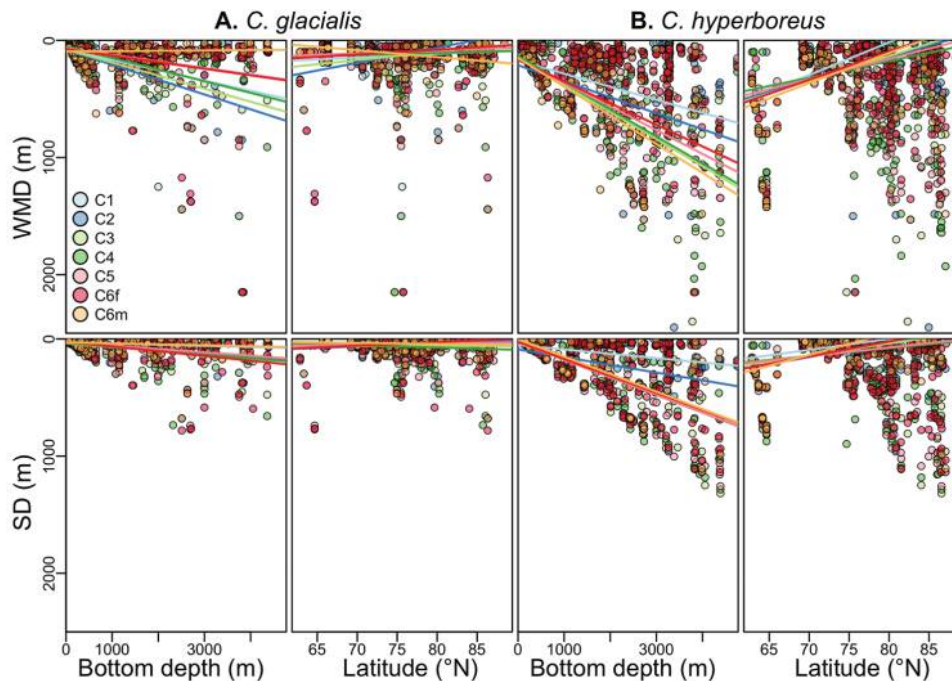


Figure 7. Weighted mean depth (WMD) and standard deviation of weighted mean depth (SD) in winter plotted against bottom depth or latitude at the sampling station for *Calanus glacialis* (A) and *Calanus hyperboreus* (B). Stage-specific estimates are displayed as colored circles. Lines show predictions from multivariate linear regression models with stage-specific WMD or SD as a function of bottom depth and latitude, with the second predictor variable set as fixed to the mean value. C1–C5, copepod stages C1–C5; C6f and C6m, female and male adult stage C6.

data show a broad depth distribution of Arctic *Calanus* (Figs. 2–6). Moreover, the highest depth-specific abundances are observed over the shelves and slopes (Figs. 2, 3). Because of warm temperatures (Maps *et al.*, 2012), high predation pressure (Bagøien *et al.*, 2001), strong advection (Aksnes and Blindheim, 1996), or lack of sufficient depths for copepods to achieve neutral buoyancy (Pond and Tarling, 2011), shelves are not considered suitable for diapause; and overwintering there may be an unsuccessful “dead end.” But recent studies suggest that, at least during winters with reduced ice coverage, food levels are sufficient to support active populations of omnivorous zooplankton, including *Calanus*, throughout the Arctic winter in many regions (Berge *et al.*, 2015a; Błachowiak-Samołyk *et al.*, 2015). Our definition of winter may be too broad in the North Atlantic (*e.g.*, the Greenland Sea, the Norwegian Sea, and the Canadian Atlantic), where the phytoplankton bloom can commence in April or earlier (Siegel, 2002), or in Arctic shelf seas such as the Barents, Laptev, and Kara Seas, where phytoplankton growth may continue until October (Falk-Petersen *et al.*, 2009). Nevertheless, the estimated WMD and SD remained variable and relatively shallow throughout the winter (Figs. 5, 6), and using a more restrictive definition (October–March) did not change the main patterns in our results. Therefore, based on this and other recent studies, we should consider the deep-basin diapause

as a facultative strategy for Arctic *Calanus*, as has been demonstrated for the Atlantic congener *Calanus finmarchicus* (Hirche, 1983; Durbin *et al.*, 1997).

Interspecific differences in depth distribution

The compiled data indicate that in winter, *C. hyperboreus* is generally found deeper and more dispersed in the water column than *C. glacialis* (Fig. 4; Table 1). This could partly be driven by differing spatial distributions: relative to total zooplankton biomass, *C. glacialis* is more dominant in shelf and slope areas, while *C. hyperboreus* dominates in the Arctic basins (Kosobokova *et al.*, 1998). Indeed, *C. glacialis* is more abundant than *C. hyperboreus* in the eastern Arctic shelves (Barents, Kara, and Laptev Seas), and the latter is absent in the shallow Chukchi Sea (Fig. 1). But although the compiled data support these spatial affinities, they also demonstrate that both species can be abundant across shelf and basin areas (Figs. 1–3). Moreover, we found significant within-station differences in WMD and SD; thus, *C. hyperboreus* tends to reside deeper than its congener in winter, independent of location.

Similarly, observations in the western Arctic Ocean and Canadian Atlantic demonstrated that *C. hyperboreus* overwinters at deeper depths than either *C. glacialis* or *C. finmarchicus*

Table 2

Regression coefficients from linear models with weighted mean depth (WMD; m) or standard deviation of weighted mean depth (SD; m) in winter as functions of bottom depth and latitude in univariate or multivariate models

Predictor response	Univariate models				Multivariate models				
	Bottom depth (m)		Latitude (°N)		Bottom depth (m)		Latitude (°N)		
	WMD	SD	WMD	SD	WMD	SD	WMD	SD	
<i>Calanus glacialis</i>	C1	0.08	0.01	4.6	2.07	0.09	0.01	-3.21	1.17
	C2	0.1	0.03	4.87	1.8	0.13	0.03	-13.02	-2.5
	C3	0.09	0.03	8.11	4.41	0.11	0.03	-7.13	-0.03
	C4	0.09	0.04	10.57	6.01	0.1	0.03	-1.8	1.95
	C5	0.05	0.02	4.32	2.45	0.06	0.03	-2.42	-1.03
	C6f	0.04	0.03	1.62	1.09	0.06	0.04	-4.08	-3.02
	C6m	0.03	0.01	5.52	1.77	0	0.01	5.84	0.89
<i>Calanus hyperboreus</i>	C1	0.07	0.02	-19.23	-6.46	0.11	0.04	-27.81	-9.32
	C2	0.1	0.05	-6.14	-5.3	0.14	0.07	-19.64	-11.83
	C3	0.18	0.12	-4.78	0.02	0.23	0.14	-21.21	-10.2
	C4	0.2	0.14	4.87	5.77	0.23	0.15	-14.19	-6.73
	C5	0.16	0.13	-1.68	4.05	0.2	0.15	-17.28	-7.46
	C6f	0.13	0.11	-12.59	-3.72	0.18	0.15	-24.04	-12.72
	C6m	0.17	0.1	-9.17	-8.5	0.25	0.15	-25.67	-18.55

Significant linear relationships ($P < 0.01$) are shown in bold.

(Ashjian *et al.*, 2003; Krumhansl *et al.*, 2018). Possibly, because of its larger lipid reserves, *C. hyperboreus* needs to descend deeper than its congeners to achieve neutral buoyancy, a presumed prerequisite for successful diapause (Visser and Jónasdóttir, 1999; Pond and Tarling, 2011). However, Krumhansl *et al.* (2018) found that despite observed differences in depth distribution, *C. hyperboreus* and *C. finmarchicus* diapause across a broad range of physical conditions (apparently tracking the coldest temperature available), without detectable interspecific differences in water temperature, salinity, or density regime.

Life history may explain some of the observed differences in depth distribution. For example, *C. glacialis* females typically spawn during the ice algal or phytoplankton spring bloom and may therefore ascend and spawn before May in some regions covered by the dataset (reviewed in Falk-Petersen *et al.*, 2009). This results in a shallower distribution in late winter than *C. hyperboreus* females, which spawn at depth. Additionally, because of its larger size, *C. hyperboreus* can remain longer in diapause (Maps *et al.*, 2014), which could influence interspecific differences in late winter. However, comparing WMD estimates per month, we found that with the exception of stages C1–C3 (for which data were limited in some months), *C. hyperboreus* is consistently distributed deeper than *C. glacialis* throughout winter (see Supplementary Fig. 2, available online).

Finally, because of its larger size, *C. hyperboreus* may need to descend deeper than its congeners to avoid being detected by visual predators (Aarflot *et al.*, 2018). Predators may influence the depth distribution of prey both *via* depth-specific predation (*e.g.*, increased mortality close to the surface) and behav-

ioral responses in the vertical distribution of prey (Kaartvedt, 1996). Disentangling the importance of these factors is difficult and requires observational data with high spatiotemporal resolution and seasonal coverage. Nevertheless, the compiled data show that *C. hyperboreus* is more abundant at depth in winter than in summer, and not only less abundant in the upper waters in winter (Fig. 3), suggesting the importance of a behavioral response.

Associations with bottom depth and latitude

We hypothesized that diapausers pursue the deepest habitat available down to a certain threshold (*i.e.*, habitats that fulfill criteria such as low light and temperature) and that, as a result, *Calanus* WMD will tend to deepen—and the depth distribution broaden (increased SD)—with increased bottom depth. In fact, both species tend to occur deeper and more dispersed with increasing bottom depth, with the strongest effect for *C. hyperboreus* (Fig. 7; Table 2). Moreover, both species tend to diapause closer to the sea bottom in shallower areas (Fig. 8; Table 3). Region-specific studies have also shown that diapausing *Calanus* tends to be found deeper and more dispersed with increased bottom depth and closer to the sea bottom at shallower locations (Dupont and Aksnes, 2012; Aarflot *et al.*, 2018; Krumhansl *et al.*, 2018). Our study suggests that on a pan-arctic scale, diapausing *Calanus* populations are blocked by shallow topography—creating potential feeding hotspots for zooplanktivores (Aarflot *et al.*, 2018).

In the central Arctic Ocean, both the vertical temperature gradient and visual predation pressure are weaker than at lower latitudes (Kaartvedt, 2008). Specifically, sea ice may

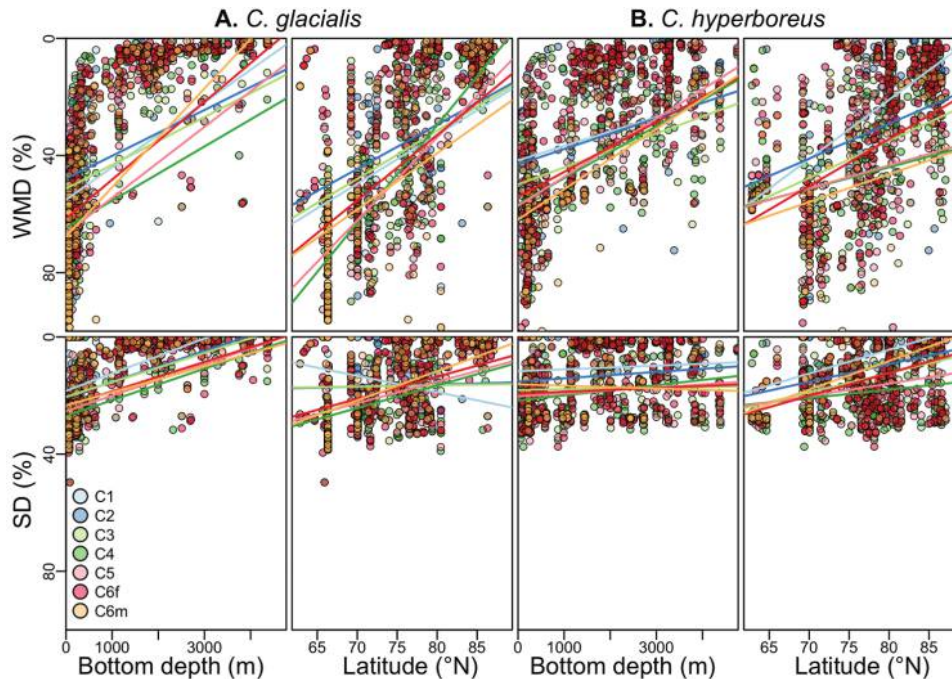


Figure 8. Weighted mean depth (WMD) and standard deviation of weighted mean depth (SD) in winter as percentage of water column depth plotted against bottom depth or latitude at the sampling station for *Calanus glacialis* (A) and *Calanus hyperboreus* (B). Stage-specific estimates are displayed as colored circles. Lines show predictions from multivariate linear regression models with stage-specific WMD (%) or SD (%) as a function of bottom depth and latitude, with the second predictor variable set as fixed to the mean value. C1–C5, copepodid stages C1–C5; C6f and C6m, female and male adult stage C6.

constrain the distribution of major predators on *Calanus*, such as capelin and herring, that gulp air at the surface to fill the swim bladder (Kaartvedt and Titelman, 2018). More generally, sea ice reduces light availability for visual predators, reducing the size-selective predation pressure on zooplankton in areas with high ice coverage (Varpe *et al.*, 2015; Langbehn and Varpe, 2017). Therefore, we expect benefits of seasonal vertical migrations to be less pronounced in regions with high ice coverage. Although regional variation in ice cover is influenced by ocean circulation, we expected to discover a general shoaling of *Calanus* diapause distribution with latitude. Indeed, we found that when accounting for the deepening of WMD with bottom depth, WMD tends to be shallower at higher latitudes, with a significant negative association between latitude and WMD for *C. hyperboreus* C2–C6 (Fig. 7; Table 2). Also, both species tend to be found closer to the sea bottom at lower latitudes (Fig. 8; Table 3). We hypothesize that these results reflect a latitudinal gradient in the incentive to descend to deep layers for diapause (potentially as a result of increased predation pressure at lower latitudes) and that this effect is strongest for the larger *C. hyperboreus*.

Additionally, our results suggest that both species tend to use more of the water column at lower latitudes (SD and latitude were negatively associated; Figs. 7, 8; Tables 2, 3). Possibly, this also reflects weaker gradients in temperature or

predation pressure with depth in the central Arctic Ocean, allowing *Calanus* to remain closer to the surface in winter. However, this appears to contradict the positive association between bottom depth and SD—presumably reflecting that increased availability of suitable diapause habitat increases the breadth of the diapausing population. Alternatively, these results may reflect that, because of lower concentration and shorter duration of food supply, *Calanus* copepods are resource limited in the central Arctic Ocean and periodically unable to store sufficient lipid reserves for diapause (Ji *et al.*, 2012; Kvile *et al.*, 2018). Recent studies suggest that a combination of external cues, internal clock mechanisms, and lipid content triggers descent to diapause and that animals without sufficient lipid reserves will remain active in the upper waters (Häfker *et al.*, 2018; Schmid *et al.*, 2018).

Another potential mechanism explaining broader vertical distribution at lower latitudes is the degree of diel vertical migration (DVM), the migration of zooplankton between the darker deep layer at daytime and the food-rich upper layer at nighttime in response to the trade-off between food availability and predation risk. As previously discussed, our winter season likely encompasses the active period for some regions, particularly at lower latitudes. Moreover, zooplankton DVM does not fully cease in winter; and stronger DVM signals are observed in lower-latitude, ice-free regions with more insolation than in higher-latitude, ice-covered regions with

Table 3

Regression coefficients from linear models with weighted mean depth (WMD; %) or standard deviation of weighted mean depth (SD; %) in winter as percentage of water column depth as functions of bottom depth and latitude in univariate or multivariate models

Predictor response		Univariate models				Multivariate models			
		Bottom depth (m)		Latitude (°N)		Bottom depth (m)		Latitude (°N)	
		WMD	SD	WMD	SD	WMD	SD	WMD	SD
<i>Calanus glacialis</i>	C1	-0.013	-0.005	-2.66	0.028	-0.011	-0.006	-1.673	0.558
	C2	-0.011	-0.005	-2.613	-0.816	-0.008	-0.005	-1.51	-0.07
	C3	-0.013	-0.005	-2.757	-0.725	-0.008	-0.005	-1.642	-0.043
	C4	-0.024	-0.009	-4.489	-1.441	-0.009	-0.005	-3.336	-0.77
	C5	-0.025	-0.009	-4.291	-1.384	-0.012	-0.005	-2.832	-0.737
	C6f	-0.022	-0.008	-3.579	-1.267	-0.013	-0.005	-2.229	-0.756
	C6m	-0.027	-0.01	-3.723	-1.474	-0.017	-0.004	-1.924	-1
<i>Calanus hyperboreus</i>	C1	-0.008	-0.002	-2.402	-0.86	-0.005	-0.001	-2.021	-0.811
	C2	-0.007	-0.002	-1.709	-0.707	-0.005	-0.001	-1.19	-0.601
	C3	-0.009	-0.002	-1.675	-0.677	-0.006	0	-1.265	-0.659
	C4	-0.01	-0.002	-1.476	-0.436	-0.009	-0.002	-0.736	-0.29
	C5	-0.012	-0.002	-1.551	-0.506	-0.01	-0.001	-0.786	-0.427
	C6f	-0.012	-0.003	-2.135	-0.819	-0.009	-0.001	-1.606	-0.778
	C6m	-0.013	-0.002	-1.638	-0.947	-0.01	0	-0.946	-0.979

Significant linear relationships ($P < 0.01$) are shown in bold.

pronounced polar night (Berge *et al.*, 2009; Hobbs *et al.*, 2018). Since we typically cannot separate day and night samples in the data compilation, a broad depth distribution could reflect DVM (although highly synchronized DVM could give the opposite result). Conversely, at higher latitudes where sea ice shading and low insolation reduce predation pressure in winter, zooplankton may aggregate close to the surface throughout the 24-hour cycle (Hobbs *et al.*, 2018).

Outlook

By synthesizing data from numerous studies, we were able to investigate variation in the depth distribution of Arctic *Calanus* in winter across gradients in bottom depth and latitude. Both *C. glacialis* and *C. hyperboreus* have a broad depth distribution in winter, indicating that parts of the population remain active. Nevertheless, both species are found deeper in winter than in summer, and the increase in WMD with bottom depth suggests that individuals seek out deep diapause habitat. In deep areas, suitable diapause habitat is available over a broad depth range, while in shallow shelves, *Calanus* is topographically blocked in winter (Genin, 2004; Aarflot *et al.*, 2018). Furthermore, our pan-arctic analysis shows that *C. hyperboreus* descends deeper than its smaller congener in winter, possibly due to a higher size-selective predation pressure. If diapause at depth primarily serves to avoid predation loss, the incentive for conspicuous copepods such as *C. hyperboreus* to seasonally migrate should be lower in the central Arctic Ocean. The negative association between latitude and *C. hyperboreus* WMD seems to support this.

Still, the inconsistency in observational data challenges our ability to draw general conclusions about the diapause habitat of Arctic *Calanus*. Data from multiple depths are required to quantify vertical variation, but a large fraction of available data are depth integrated or from single intervals (Fig. 1). Multiple-net systems for zooplankton sampling are ideal for this purpose but typically require larger ships and more time for sample processing than simpler nets (Skjoldal *et al.*, 2013). Moreover, if diapause layers are aggregated close to the sea floor (Auel *et al.*, 2003), they will be underestimated by most sampling gear.

Unsurprisingly, more data are available from near-shore shelf areas than slopes and basins. To improve our understanding of the life cycle of Arctic *Calanus* species, we call for more consistent sampling efforts in the central Arctic. In particular, slopes may be important diapause habitat supplying *Calanus* biomass to the shelves, but data from these areas are scarce. Several recent studies have focused on zooplankton dynamics during the Arctic winter (Berge *et al.*, 2015b and references therein), and we encourage continued efforts to improve our knowledge of the role of diapause in the abundant *Calanus* copepods.

Acknowledgments

KØK was supported by the Woods Hole Oceanographic Institution John H. Steele Postdoctoral Scholar award and the VISTA Scholarship (<http://www.vista.no>). We are grateful to Sigrún Jonasdóttir, Susan Mills, Imme Rutzen, Russ Hopcroft, Peter Munk, and Rasmus Swalethorp for kindly

sharing observational data. We would like to thank two anonymous reviewers for insightful and constructive suggestions that helped us improve the manuscript.

Data Accessibility

Compiled observational data used in the study are available online at arcticdata.io/catalog/#view/doi.org/10.18739/A2KD1QK3Q. R code and data to run all analyses are available online at github.com/kristokv/calanus_diapause_depth.

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