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Sea ice decline drives biogeographical shifts of key *Calanus* species in the central Arctic Ocean

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Abstract

In recent decades, the central Arctic Ocean has been experiencing dramatic decline in sea ice coverage, thickness and extent, which is expected to have a tremendous impact on all levels of Arctic marine life. Here, we analyze the regional and temporal changes in pan-Arctic distribution and population structure of the key zooplankton species *Calanus glacialis* and *C. hyperboreus* in relation to recent changes in ice conditions, based on historical (1993–1998) and recent (2007–2016) zooplankton collections and satellite-based sea ice observations. We found strong correlations between *Calanus* abundance/population structure and a number of sea ice parameters. These relationships were particularly strong for *C. glacialis*, with higher numbers being observed at locations with a lower ice concentration, a shorter distance to the ice edge, and more days of open water. Interestingly, early stages of *C. hyperboreus* followed the same trends, suggesting that these two species substantially overlap in their core distribution area in the Arctic Ocean. *Calanus glacialis* and *C. hyperboreus* have been historically classified as shelf versus basin species, yet we conclude that both species can inhabit a wide range of bottom depths and their distribution in the Arctic Ocean is largely shaped by sea ice dynamics. Our data suggest that the core distribution patterns of these key zooplankton are shifting northwards with retreating sea ice and changing climate conditions.

KEYWORDS
biogeography, climate change, phenology, polar regions, zooplankton

1 | INTRODUCTION

Copepods of the genus *Calanus* commonly dominate the biomass of zooplankton in temperate and polar seas and serve as a critical link between microbial primary/secondary production and higher trophic levels, such as fish, birds and marine mammals (Dahl et al., 2003; Falk-Petersen et al., 2009). In the Arctic Ocean, *Calanus* are represented by three species, two of which, *C. glacialis* and *C. hyperboreus*, are resident to the Arctic, and one, *C. finmarchicus*, is an expatriate advected with currents from the North Atlantic (Conover, 1988; Hirche & Kosobokova, 2007; Kosobokova, 2012; Wassmann et al., 2015).

In recent decades, climate patterns in the Arctic Ocean have been undergoing changes that are unprecedented in modern history,

the most apparent of which is the dramatic reduction of sea ice. The Arctic sea ice is becoming younger (Comiso, 2012) and thinner (Kwok et al., 2009), with more and more area becoming seasonally ice covered, leading to changes in the surface water properties and affecting surface circulation patterns (Polyakov et al., 2018, 2020). The importance of sea ice in the life cycles of zooplankters, including *Calanus*, has been well documented (Bluhm et al., 2011; Ehrlich et al., 2020; Flores et al., 2019; Runge & Ingram, 1991; Werner & Hirche, 2001), and it is fully expected that the aforementioned changes will be reflected in the communities and organisms living beneath the ice (Leu et al., 2011; Søreide et al., 2010).

The pronounced reduction in sea ice extent, together with increasing influence of Atlantic and Pacific waters advected into the Arctic (a process recently defined as borealization, Polyakov et al., 2020), has caused many documented northward shifts in distribution of sub-Arctic species across all trophic levels (see review in Polyakov et al., 2020). Similarly, many Arctic species have retreated farther north (Dalpadado et al., 2012; Eriksen et al., 2017; Orlova et al., 2015; Zhukova et al., 2009). The changes in temperature and primary production patterns are also affecting the phenology of organisms. For example, the boreal *C. finmarchicus* reaches a later developmental stage in warmer years in the Fram Strait region through shifts in timing of reproduction and accelerated growth at higher temperatures (Weydmann et al., 2018).

Of the two Arctic *Calanus* species, *C. hyperboreus* is typically considered to be a deep basin (oceanic) species with its core distribution area lying in the Greenland Sea and central Arctic Ocean, whereas *C. glacialis* is classified as an Arctic shelf (neritic) species (Conover, 1988; Hirche & Mumm, 1992; Jaschnov, 1970; Kosobokova, 2012) found in Arctic marginal seas with bottom depths of 50–200 m. Typically, both species compose 80%–90% of total mesozooplankton biomass in their respective environments (Kosobokova, 2012; Kosobokova & Hirche, 2009). *Calanus glacialis* generally has a 1 or 2 year life cycle (Conover, 1988; Kosobokova, 1999), developing from eggs to wax ester-rich copepodite stages C4 and C5 within a single year (Scott et al., 2000), and can utilize both lipid reserves and available food to initiate reproduction (Daase et al., 2013). On the contrary, the larger *C. hyperboreus* takes 3–4 years to reach maturity, with mating and reproduction taking place at depth during the winter months using lipid reserves. During the first year, this species reaches the C3 copepodite stage, which is the first overwintering stage for this species in the central Arctic (Conover, 1988; Hirche, 1997), although in other regions it can reach later stages if environmental conditions allow it (Falk-Petersen et al., 2009). The first naupliar stages of both species do not feed, with N3 being the first feeding stage (Conover, 1988; Jung-Madsen et al., 2013). Although *Calanus* is among the best-studied marine organisms in high latitudes, many unanswered questions remain about the mechanisms that drive the distribution of the different species of the complex.

In the Arctic Ocean, the biomass of *C. glacialis* peaks around the shelf break of the marginal shelf seas and declines rapidly in the deep Arctic Basin (Kosobokova, 2012; Kosobokova & Hirche, 2009; Wassmann et al., 2015). Egg production experiments conducted in

the 1990s found that reproduction of *C. glacialis* was restricted to the outer shelf and slope of the Arctic Ocean, with no eggs produced by individuals remaining under pack ice in regions deeper than 500 m (Ashjian et al., 2003; Kosobokova & Hirche, 2001). The observed populations of *C. glacialis* in the central Arctic Ocean have been mainly composed of late stage individuals, C5 copepodites-adults, with no early life stages present (Ashjian et al., 2003; Kosobokova et al., 1998; Kosobokova & Hirche, 2001), suggesting expatriation. Nonetheless, modeling studies have suggested that ice retreat will cause *C. glacialis* to expand its range poleward in the next 30 years (Feng et al., 2016, 2018; Ji et al., 2012). During the 2016 expedition PS101 of the RV *Polarstern* to the Arctic Ocean, we observed early life stages of *C. glacialis* for the first time in the central Amundsen Basin at 87°N latitude in a region covered with loose 1.5 m-thick ice. This observation, to our knowledge, is the first empirical evidence in support of the aforementioned modeling studies.

We hypothesized that the degrading ice conditions may allow this species, which has been thought to be restricted in its reproduction to the shelf and slope, to expand its range farther into the deep basins. We explore this hypothesis by examining an extensive zooplankton dataset spanning three decades, which includes two periods: earlier ice-covered years with more "typical" ice conditions (1993–1998) (Haas & Eicken, 2001) and recent years with a reduced ice cover (2007–2016) (Slater et al., 2021). We use these data to analyze the pan-Arctic distribution and population structure of *C. glacialis* and *C. hyperboreus* and investigate how these trends are related to sea ice conditions.

2 | METHODS

2.1 | Zooplankton data

Abundance, biomass, and population structure of *C. glacialis* and *C. hyperboreus* were examined using zooplankton counts from nine expeditions to the central Arctic Basin, with four from the 1990s (64 stations), and five from the 2000 to 2010s (54 stations) (Figure 1; Table S1). All expeditions took place during the summer–autumn months, from late July to early October. Zooplankton samples were collected with a HydroBios MultiNet Midi (1993–1996), MultiNet Maxi (1998–2016) or a closing Juday net (2015) with a 150 um mesh size in the whole water column down to the seafloor at standard depth intervals (sea floor – 1000, 500, 200, 100, 50, 0 m), and preserved in 4% borax- or hexamine-buffered formalin (for more sampling details, see Ershova & Kosobokova, 2019; Kosobokova & Hopcroft, 2010; Kosobokova et al., 2011). *Calanus* specimens in most cases were counted from the entire sample or, when very abundant, from a quantitative sub-sample, under a stereo microscope. The prosome length of *Calanus* specimens was measured from the tip of the cephalosome to the distal lateral end of the last thoracic segment with a resolution of 25 μm. The species were distinguished according to the size ranges shown in Table S2. *C. finmarchicus* and *C. glacialis* can overlap in their size distribution in some areas, but within
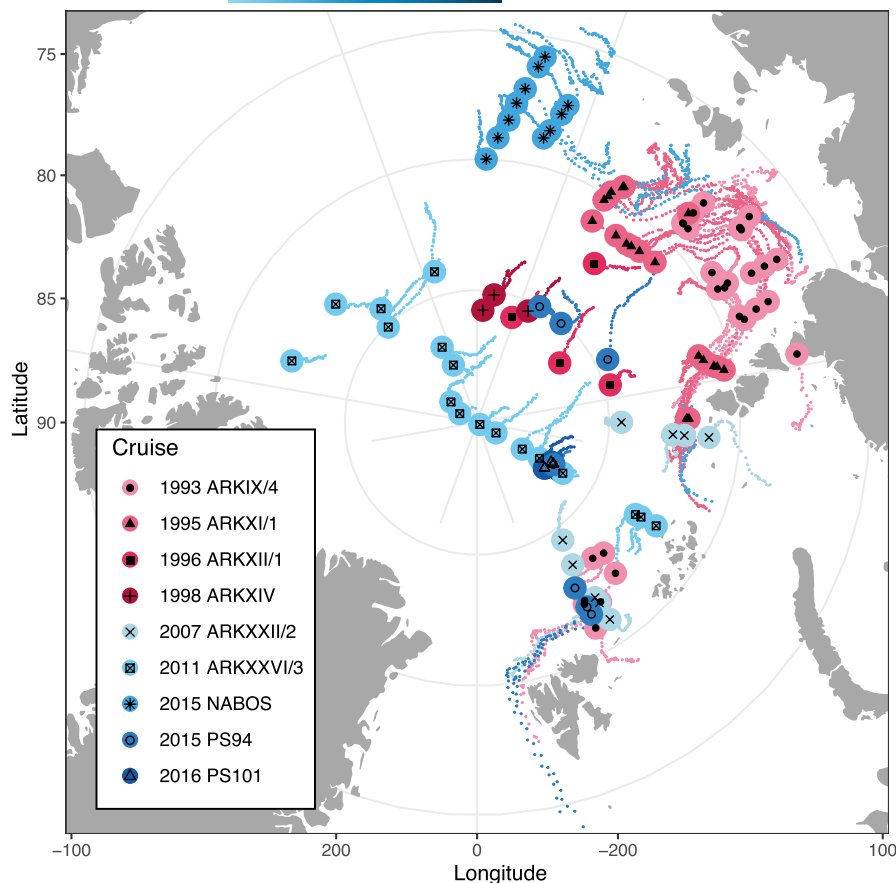
FIGURE 1 Map of zooplankton stations used in analyses, with shades of red representing 1993–1998 expeditions and shades of blue 2007–2016 expeditions. Tracks indicate drift of surface 50 m water layer 6 months prior to sampling

the Central Arctic they generally fall within distinct size classes (Choquet et al., 2018). Abundances were calculated per unit (1 m^2) area. Biomass (g DW m^{-2}) was calculated using a known length–mass regression relationship for *Calanus* (Hirche & Mumm, 1992; Madsen et al., 2001). Although for a small subset of the stations count data was available only for the surface 0–100 m layers, we assume that we captured most of the *C. glacialis* population, since in the summer months most individuals are generally found in the upper 100 m (Ashjian et al., 2003; Geynrikh et al., 1983; Kosobokova, 2012). Since *C. hyperboreus* is often found also at greater depths (Ashjian et al., 2003; Dawson, 1978; Geynrikh et al., 1983; Kvile et al., 2019), for analysis of this species, we excluded deep stations for which data were not available for the whole water column. We also excluded stations with a bottom depth shallower than 100 m.

2.2 | Sea ice data

Sea ice data were obtained from the Nimbus-7 SMMR and DMSP SSM/ISSMIS Passive Microwave Data set, which provides daily satellite-derived sea ice concentrations on a 25 km grid (Cavalieri et al., 1996). Each station was assigned to a cell on the grid, and sea ice concentrations for each station were obtained for a period of 180 days prior to sampling and 30 days post sampling. However, as plankton is not stationary, but drifts with the water masses, each "station" was treated not as a fixed point, but as a trajectory

(Figure 1). The approximate drift of the community found at each station was estimated using particle tracking in a 14-year (2004–2017) hindcast of the SINMOD model (Armstrong et al., 2019; Slagstad et al., 2015). This implementation of SINMOD spans the Central Arctic Basin and Atlantic gateway regions with a horizontal resolution of 20 km, on a z grid (25 layers total, 15 in the top 500 m). Particles were tracked using 0–50 m average currents, and therefore are more reflective of movement of the surface-dwelling *C. glacialis* than the deeper-dwelling *C. hyperboreus*. Trajectories were calculated forward in time, used the midpoint method with a timestep of 2 h, for a high-resolution grid of starting locations, and then the trajectory passing closest to each sample in latitude, longitude, and date was selected as the "advective history" of that sample. For samples after 2004, we calculated the trajectory using the appropriate year from the SINMOD hindcast. For samples from the 1990s, prior to the start of the available hindcast, we calculated a trajectory for each sample location for the appropriate yearday in each of 2004–2017, thus producing a small ensemble of possible advective histories, and then selected the single trajectory closest to the median of that ensemble. Finally, sea ice concentrations were interpolated along these histories.

Using the values of sea ice concentration, a list of ice variables was generated (Table 1) for each station. For the stations within the "pole hole" (area around the north pole unreachable by satellite), sea ice concentration at the time of sampling was obtained from ship records, and the integrated values were not calculated. Additionally,

TABLE 1 List of variables used in analyses, extracted for 180 days prior to and 30 days post-sampling

Variable name	Variable value
Ice.conc	Sea ice concentration at time of sampling (smoothed over 5 days)
Distance.edge	Distance (km) to ice edge at time of sampling
Days.ice.cover	Number of days location was ice covered (>15% cover)
Days.ice.marg	Number of days location was within the marginal ice zone (1–15% ice cover)
Days.ice.less.50	Number of days with <50% ice cover
Days.ice.100	Number of days with >99% ice cover
Ice.min	Minimum ice concentration at location during last 180 days

we examined the effect of bottom depth (m) and distance to the continental slope, defined as the shortest path to the 500 m isobath with negative and positive values indicating on- and off-shelf locations, respectively. Bathymetry data were obtained from ETOPO1 database from NOAA (Amante & Eakins, 2009). Chlorophyll *a* values (µg L^{-1}) for the corresponding expeditions were obtained from published datasets on PANGAEA (Nöthig, Boetius, et al., 2015; Nöthig, Kuckero, et al., 2015; Nöthig, Petersen, et al., 2018; Nöthig, Strache, et al., 2018; Nöthig & Lorenzen, 2015). Those were integrated across the upper 50 m (Mean.Chl).

2.3 | Statistical analysis

All analyses were conducted in R (R Core Computing Team, 2017). Correlations between *Calanus* abundance, biomass and sea ice parameters were investigated using linear mixed effects models using the R package nlme (Pinheiro et al., 2020), with the random factors including "Expedition" (to include variability of sampling and geography) and "Day of Year" (to account for seasonal differences in sampling). As the latter term was insignificant (Table S3), it was removed from the model, with only "Expedition" remaining a random factor. Abundance values were log-transformed to conform to a normal distribution. All explanatory variables were scaled to ensure comparability of the estimated effect. The relationships were examined visually for non-linearity and additional transformations (logarithmic or polynomial) were introduced to improve the model. Due to the very different spatial coverage of the expeditions, inter-annual comparisons were not conducted. However, in addition to running the combined dataset, we also examined the two time periods individually (1993–1998 and 2007–2016) to determine if the trends were consistent between them. The best subset of variables was selected using a forward model selection using AIC (Akaike information criterion) values. The coefficients of determination (variance explained by the model) were obtained using the R package PiecewiseSEM (Lefcheck, 2016), where the marginal R^2 (R^2_{marg}) is the variance explained by the fixed factors alone, whereas the conditional R^2 (R^2_{cond}) is variance explained by both fixed and random factors (Nakagawa &

Schielzeth, 2013). In addition to overall species abundance, we also examined the correlations of environmental parameters to abundances of individual developmental stages. For *C. glacialis* these included three groups: C1–C2 (recently produced individuals); C3–C4 (current year individuals at potential diapausing stages); and C5–C6 (the previous year's generation). For *C. hyperboreus*, we included four groups to account for differences in the life cycles between the species: C1–C2 (recently produced individuals); C3 (first diapausing stage), C4–C5 (second diapausing stage from previous year); and C6 (individuals three years or older).

The effects of sea ice parameters on the population structure of *C. glacialis* and *C. hyperboreus* were investigated using canonical correspondence analysis (CCA) from the R package vegan (Oksanen et al., 2016), using a matrix of untransformed proportions of each developmental stage (C1–C6) at each station and scaled environmental variables. The best subset of variables resulting in the highest inertia (variance explained) by the model was selected using stepwise selection using adjusted R^2 as a selection criterion with the function ordiR2step. The significance of the model and individual terms was analyzed using permutation tests at a significance level of $p < 0.05$. We also examined differences in population structure between the two time periods (1993–1998 and 2007–2016) by correlating the ordination to the variable "Period" using the function envfit (Oksanen et al., 2016) and examining the locations of the centroids for the two groups on the resulting ordinations.

3 | RESULTS

3.1 | Sea ice characteristics

A wide range of sea ice conditions was encountered at the time of sampling, varying from entirely open water to complete ice coverage (Figure 2a), and mean annual ice cover ranging from ~30% to near 100% (Figure 2b). The distance from the sampling location to the ice edge ranged from –120 to 1000 km (with negative values indicating locations in open water) (Figure 3b). All stations within the deep basins of the Arctic Ocean were ice covered throughout the entire year, while the stations around the slope and outer shelf had 10–130 open water days (data not shown) during the previous 6 months. However, the number of days of full ice cover (>99%) was more variable between the deep stations, with locations in the Amerasian Basin having more full ice cover days than those in the Eurasian Basin, particularly those sampled during recent years (2015–2016) (Figure 2c). Similarly, most deep stations had zero days with <50% ice cover, with the exception of the stations sampled in 2015 and 2016 and one station sampled in 1995 (Figure 2d). The sea ice minimum during the sampling year within the deep basins ranged from 50% to 80%, while the stations sampled during 2015–2016 stood out as having a much lower minimum sea ice concentration of ~30% (data not shown). The sea ice concentration at time of sampling was highly correlated ($r = 0.86$) with the local ice minimum for the year, which is unsurprising, given that most sampling was conducted in
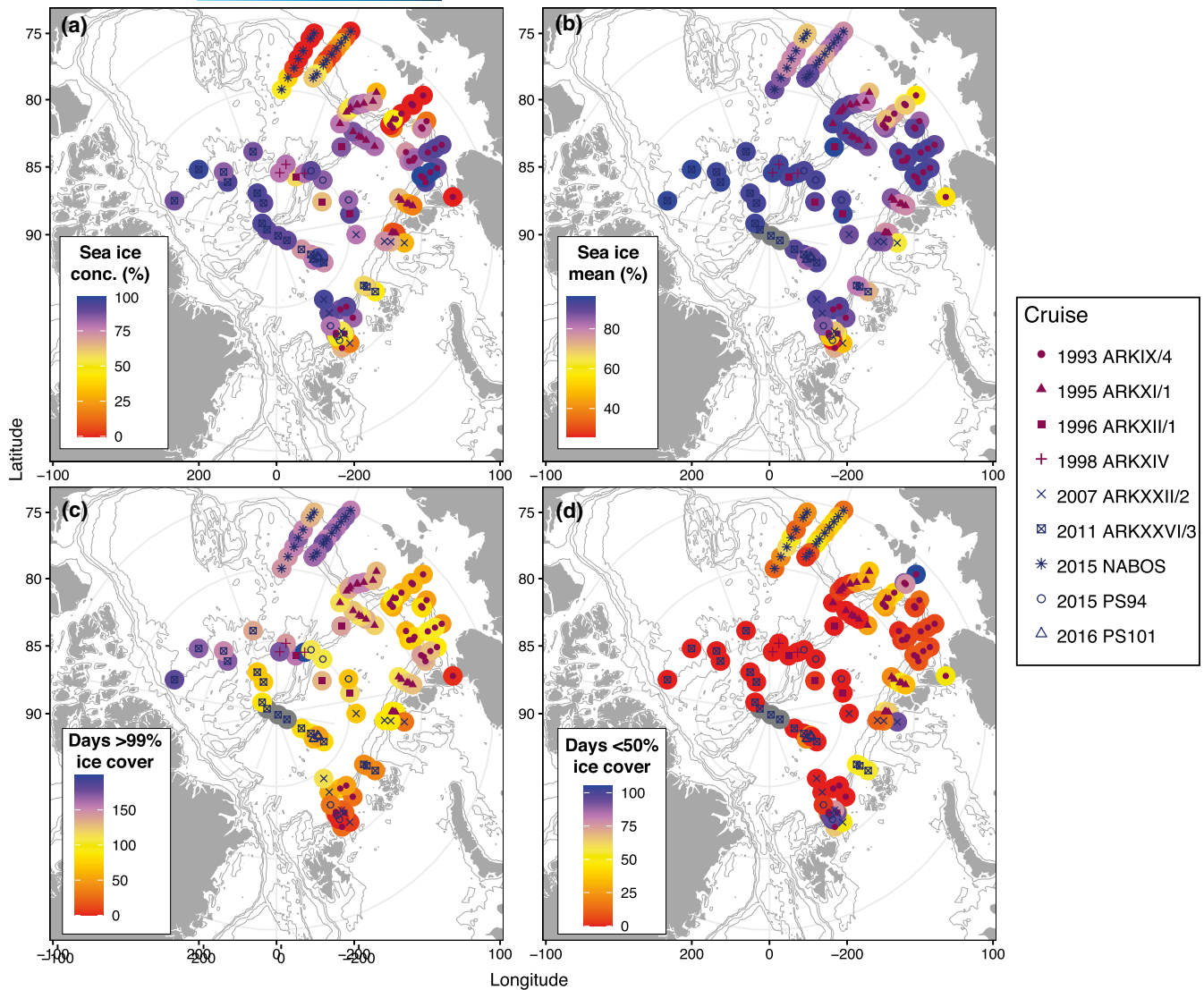
FIGURE 2 Select sea ice characteristics of the sampled locations. (a) Sea ice concentration (%) at time of sampling; (b) annual sea ice mean concentration (%) during the sampling year; (c) number of days (/210) with 100% ice cover; (d) number of days (/210) with <50% ice cover. Symbols indicate expedition with shades of red corresponding to 1993–1998 expeditions and shades of blue to 2007–2016 expeditions. Gray symbols indicate stations within the "pole hole" for which satellite data are unavailable

August–September, when the ice cover in the Arctic is at its lowest. The sea ice extent during ice minimum was substantially reduced in the later sampling years compared to the early ones (Figure 3a). The distance from sampling location to the 500 m isobath showed a strong linear correlation to distance to the ice edge ($r = 0.92$), and the ice edge was located, on average, approximately 100 km farther than the shelf break. Relative to the 1993–1998 time frame, the 2007–2016 period showed a reduction of this distance by 50–100 km (Figure 3b).

3.2 | Distribution of *C. glacialis* and *C. hyperboreus*

Calanus glacialis was present at every station, and *C. hyperboreus* was observed at nearly all stations deeper than 100 m (Figure 4). The highest abundances of *C. glacialis* were generally observed on the outer shelf and slope and the lowest values in the central basins, although among the shelf/slope stations the variability was extremely high. Overall, the values spanned over 3 orders of magnitude, ranging from <1000 to >100,000 ind m^{-2} (mean 8000 ind m^{-2}). The biomass of *C. glacialis* generally followed the abundance trends, although the variability was less pronounced, with values ranging from 0.02 to 7 g DW m^{-2} (mean 0.8 g DW m^{-2}) and spatial patterns were more visible, with a distinct band of elevated biomass observed around the outer shelf. The highest abundance values were observed during 2007–2016 time period, although the highest biomass was registered during the 1993–1999 period (Figure 4a,b). Abundances of *C. hyperboreus* were generally significantly lower than for *C. glacialis*, with values no higher than 10,000 ind m^{-2} (mean 1000 ind m^{-2}), and the variability in the abundance was also much lower. The biomass of *C. hyperboreus*, on contrary, was generally higher than that of *C. glacialis*, especially in the central basins, with values up to 10 g DW m^{-2}
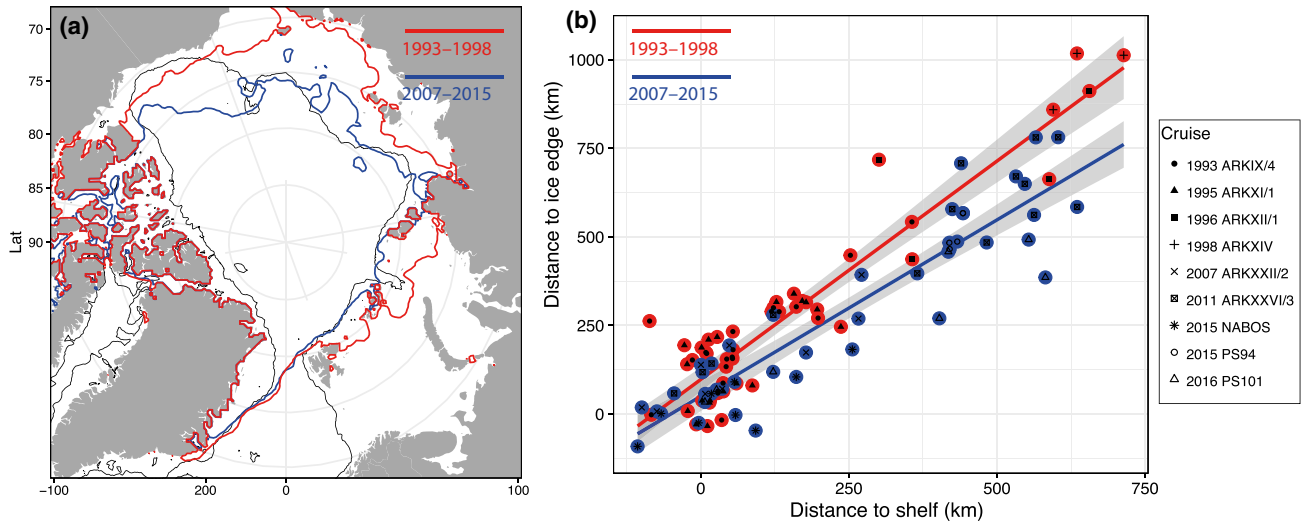
FIGURE 3 (a) Average minimum sea ice extent during the 1993–1998 vs. the 2007–2016 periods; (b) distance to the ice edge vs. distance to the shelf (km) at stations sampled in 1993–1998 (red) vs. 2007–2016 (blue)
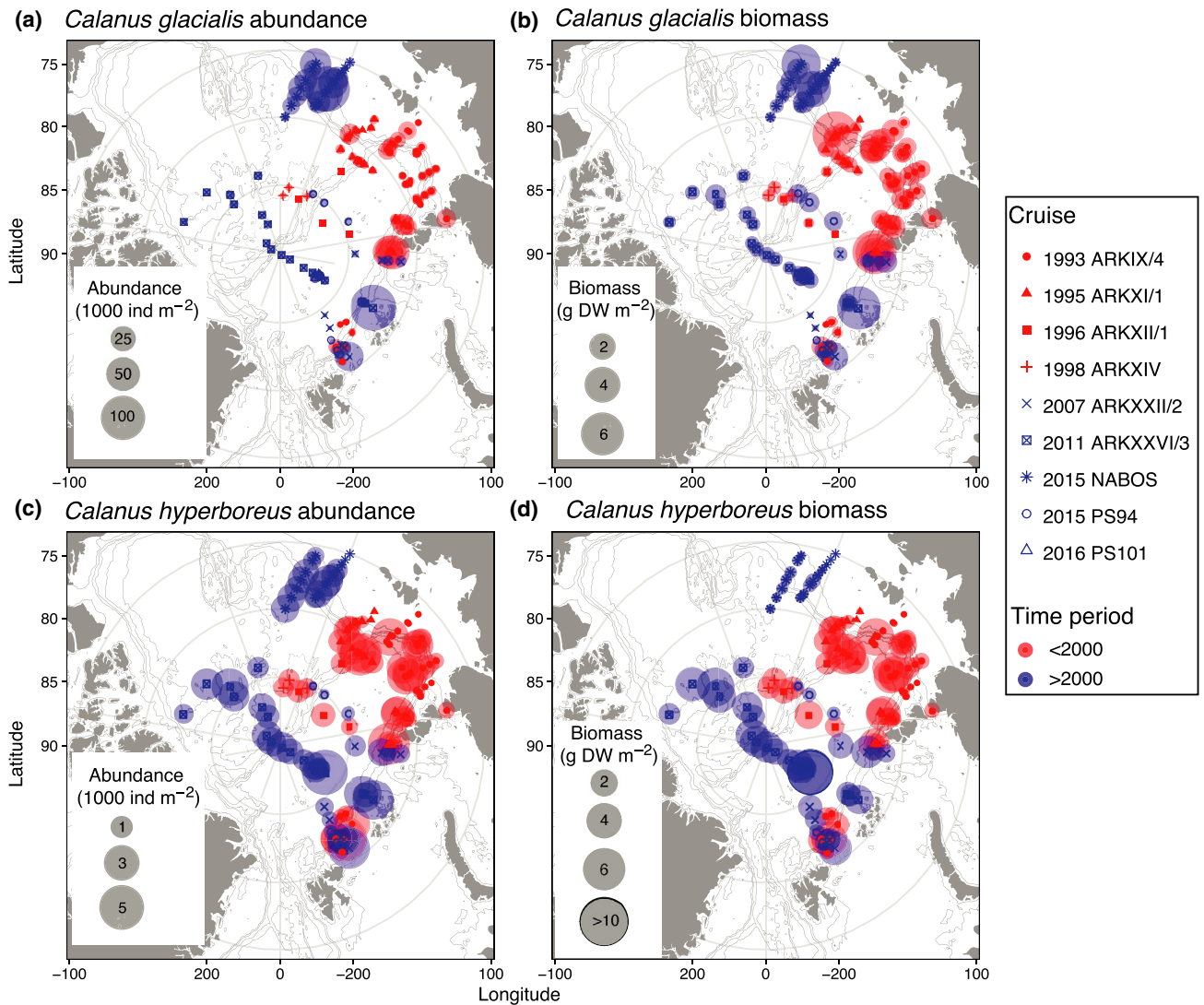

FIGURE 4 Abundance (a, c) and biomass (b, d) of *Calanus glacialis* and *C. hyperboreus* in the Arctic Ocean during 1993–1998 (red) and 2007–2016 (blue)

(mean 2 DW m^{-2}). Nonetheless, some of the highest values of both abundance and biomass of *C. hyperboreus* were also observed on the outer shelf and slope, despite the shallower depths at those locations (Figure 4c,d).

3.3 | Relationship of *Calanus* abundance to sea ice parameters

Several variables were significantly ($p < 0.01$) correlated with total *C. glacialis* abundance in the upper 100 m during both time periods, including most of the sea ice parameters, depth and distance to shelf break (Figures 5 and 6a; Table S3). Among these variables, the strongest correlations were observed for the sea ice parameters, especially sea ice concentration at the time of sampling (negative, $R^2_{marg} = 0.45$; Figure 5b), distance to the ice edge (negative, $R^2_{marg} = 0.44$; Figure 5e), and the number of days with less than 50% ice cover (positive, $R^2_{marg} = 0.38$; Figure 5d). The relationships were remarkably similar when the two time periods were examined

independently, with generally no significant differences in slope or intercept. Several of the observed relationships were not linear; for example, abundance dropped rapidly in the first 200 km away from the ice edge and flattened out at higher distances (Figure 5e). Similarly, abundance increased with the number of days with <50% ice cover until ±50, after which it began declining again during the 2007–2016 time period (Figure 5d) (notably, there were no stations with over 60 days with <50% cover during the 1993–1998 sampling period). Although the distance to shelf break and distance to the ice edge were highly correlated, *C. glacialis* abundance showed a much stronger relationship to the latter ($R^2_{marg} = 0.44$) than the former ($R^2_{marg} = 0.18$) (Figure 5e,f). This difference becomes even more apparent when examining the two time periods separately: although the observed relationship between abundance and distance to ice edge was nearly identical during both time periods, the correlation to distance to shelf was much less pronounced during the later study years ($R^2_{marg} = 0.26$ vs. 0.07) (Figure 5f). A weak positive relationship was also observed to mean chlorophyll concentration ($p < 0.01$, $R^2_{marg} = 0.07$, Figure 6a).
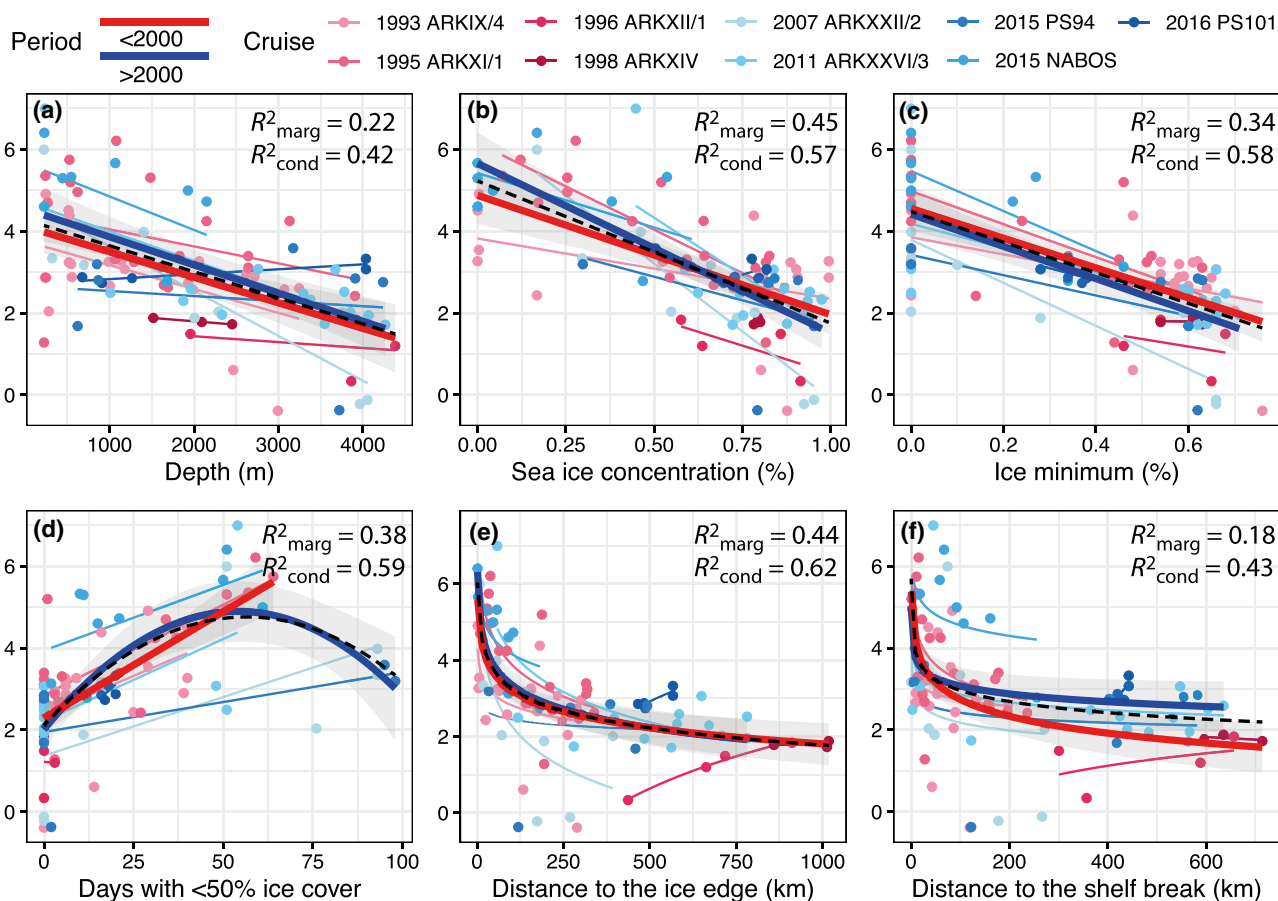

FIGURE 5 Mixed effect model results of relationships between *Calanus glacialis* abundance (log-transformed) and (a) depth, (b) sea ice concentration at time of sampling, (c) ice minimum, (d) days with <50% ice cover, (e) distance to the ice edge and (f) distance to the shelf break. Colors indicate different expeditions (color code same as on Figure 1); thin lines show trends within each expedition; thick lines shows averaged linear trend for 1993–1998 period (red) and 2007–2016 (blue). Black dashed line and R^2 values correspond to the averaged trend across the whole period. A second-degree polynomial transformation was applied to the predictor data for days with <50% ice cover, and a log-transformation for distance to the ice edge and distance to the shelf break
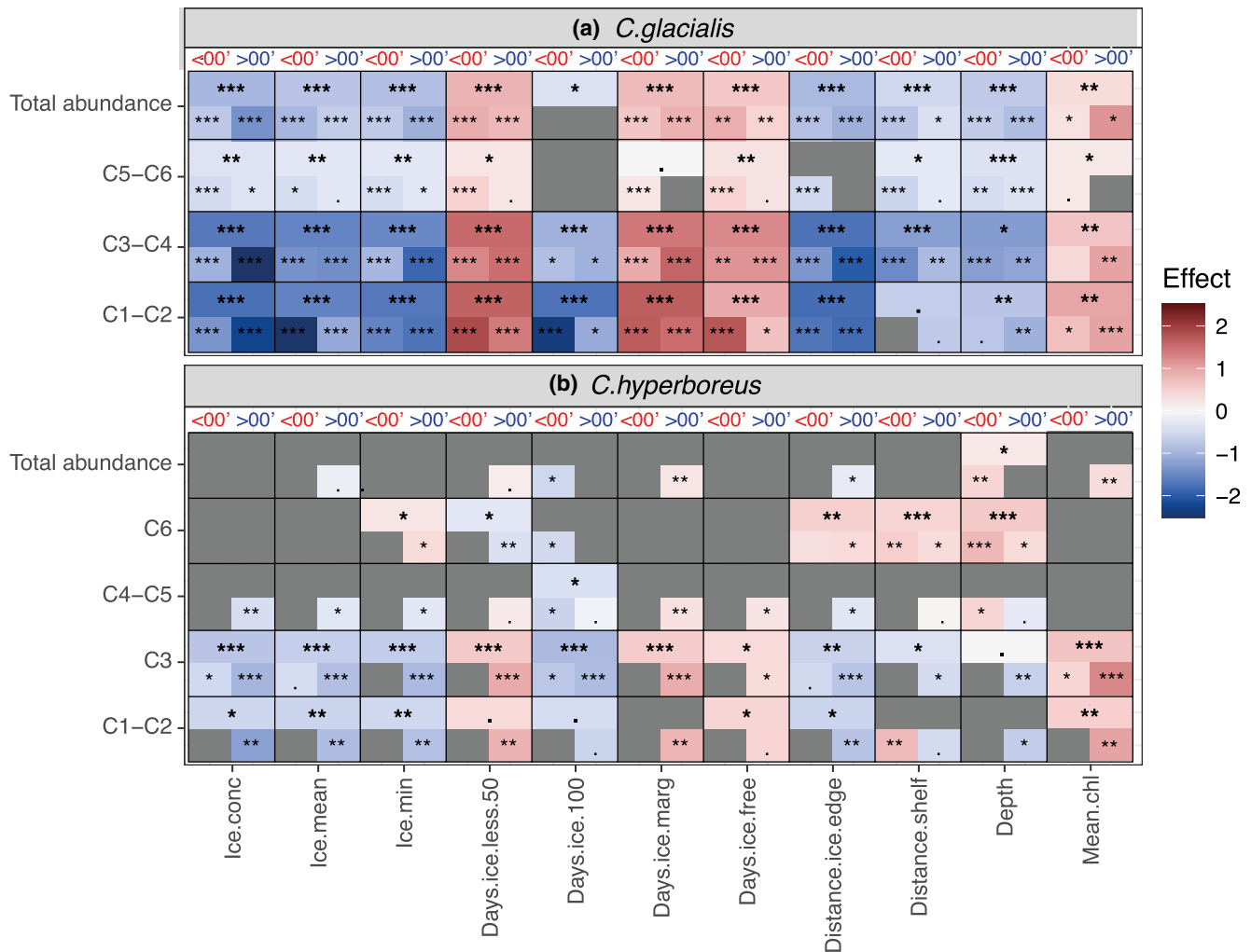
FIGURE 6 Effects of scaled ice/physical variables on overall/individual stage abundances of (a) *Calanus glacialis* and (b) *C. hyperboreus* via mixed model results. The upper part of each cell shows the averaged trend across the entire dataset; bottom part shows trends for 1993–1998 (<00') and 2007–2016 (>00') periods. Color intensity shows the strength of the relative effect of each variable, with red indicating a positive correlation and blue, a negative one. Stars indicate *p* value: ***<0.001; **<0.01; *<0.05; –0.1. Gray tiles indicate no significant relationship

The best multiple mixed linear model explaining *C. glacialis* abundance included sea ice concentration, the number of days with <50% ice cover, and depth, with the greatest relative effect observed for sea ice concentration ($R^2_{marg} = 0.58$, $R^2_{cond} = 0.65$). When abundances of individual developmental stages were examined separately as C1–C2 (recently produced new generation (current year) individuals); C3–C4 (current year individuals developing to potential diapausing stages); and C5–C6 (previous year generation individuals), the correlations varied slightly (Figure 6a). In particular, C1–C2 copepodites showed the strongest correlations to all examined sea ice variables, especially sea ice concentration, distance to the ice edge, and the number of days that the station was in the marginal ice zone. They also showed the weakest relationship to depth and distance to the ice edge. Abundances of C5–C6 copepodites showed the weakest trends in relation to all examined parameters. Similar to overall abundance, the relationships of copepodite abundances to sea ice/environmental parameters were generally similar in significance and magnitude during the two time periods, although a few of the

variables showed a much stronger correlation during one or the other period (Figure 6a).

Overall *C. hyperboreus* abundance was not significantly correlated to any of the environmental variables, with the exception of a slight positive relationship to depth (Figure 6b; Table S3). When developmental stages were examined separately, abundances of early life stages (C1–C2), and especially C3 of *C. hyperboreus*, revealed similar, albeit slightly weaker, trends as compared to *C. glacialis*, showing significant relationships to a number of ice-derived variables, with higher abundances found at lower ice concentrations and higher numbers of ice-free days (Figure 6b). The abundances of early life stages showed a weak relationship to chlorophyll *a* concentrations and no relationship to depth or the distance to the shelf break (Figure 6). Abundances of C4–C5 showed no relationship to any of the examined variables; however, abundances of adults (C6, females and males) showed opposite trends as compared to early life stages, with higher abundances associated with heavier ice, greater depths, and farther distance from the shelf break. The

contrasting directions of the trends between early developmental stages and adults explain the lack of observed correlations of the overall species abundance to the examined parameters. In contrast to *C. glacialis*, the relationships observed for early copepodites of *C. hyperboreus* to ice/environmental parameters during the 2007–2016 period were much stronger than during the 1993–1998 sampling period (Figure 6). This can be partly explained by scarcity of data for these stages during the earlier period, as very few young

copepodites of *C. hyperboreus* were observed during this time (see section below).

3.4 | Population structure

The developmental stage composition of *C. glacialis* population was highly variable spatially (Figure 7a). The central basins stations, with
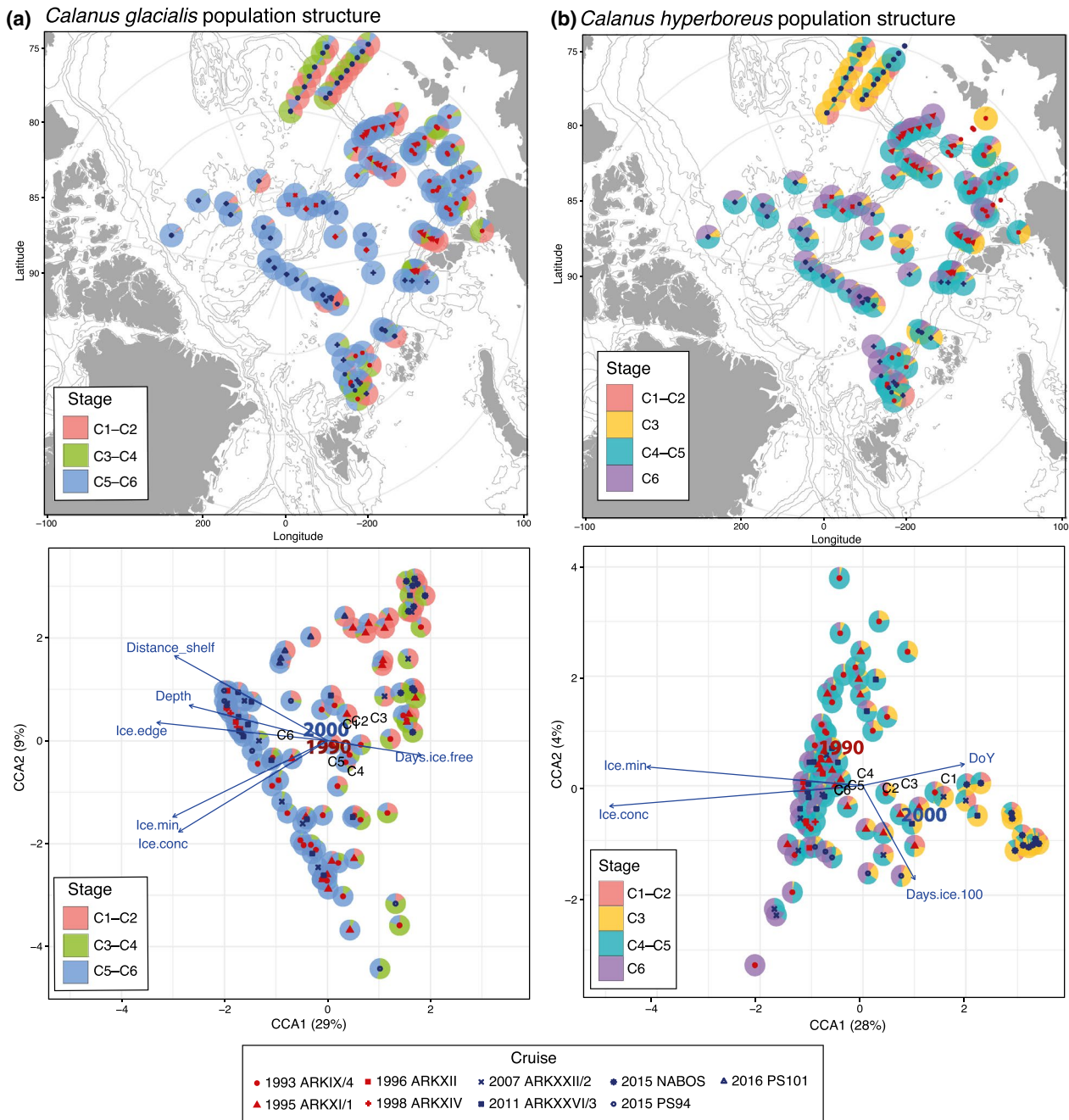

FIGURE 7 Population structure (developmental stage composition) and canonical correspondence analysis (CCA) of relative developmental stage abundance of (a) *Calanus glacialis* and (b) *C. hyperboreus*. Symbols indicate expedition with symbol color corresponding to sampling period (1993–1998 – red; 2007–2016 – blue). Arrows show constraining variables with length representing strength of the correlation to the ordination. C1–C6 symbols indicate centroids for each developmental stage; 1990/2000 symbols indicate centroids for the 1993–1998 and 2007–2016 periods, respectively

a few exceptions, were heavily dominated by the previous year generation, that is, older copepodite stages (C5-adult females). On the shelf and slope, a higher presence of early life stages C1–C2 and potential first year diapausing stages C3–C4 was observed, but their relative contribution varied between locations, and many of the shelf/slope stations were also dominated by later stage individuals. The best canonical correspondence analysis (CCA) model of relative stage composition ($p < 0.01$) included distance to the ice edge, ice concentration at time of sampling, local ice minimum, number of days the location was ice-free, and distance to shelf as constraining factors (Figure 7a; Table S4). This model explained 42% of total inertia in the relative developmental stage composition at each station, with most of the explained variability (29%) found along the first axis. The highest proportion of the variance (23%) was explained by distance to the ice edge, followed by sea ice concentration (7%). Higher proportions of early (C1–C4) stages were positively correlated with the number of days the location was the marginal ice zone and negatively correlated with sea ice concentration. Stations dominated by C5–C6 stages were observed at the deepest regions farthest from the ice edge/shelf break, and with the highest sea ice concentrations. The centroids for the two time periods were very close together, near the center of the ordination, indicating that the overall stage composition was similar during both periods in the examined data.

Patterns in the developmental stage distribution of *C. hyperboreus* generally followed those of *C. glacialis*, when taking into account the differences in life cycles between the two species (Figure 7b). The basin stations were dominated by previous year's stages C4–C6, with a very low contribution of copepodites C1–C3, produced during the current year. The first diapausing stage, C3, was present in very low numbers in the basins, and the highest relative proportions of this stage were found on the slope stations, especially on the two transects north of the East-Siberian Sea. Early copepodites C1–C2 generally composed a small percentage of the population. The CCA constrained by sea ice concentration, minimum ice cover, number of days with 100% ice cover, and DoY (Day of Year) explained 33% of total inertia in the data ($p < 0.01$) (Figure 7b; Table S4) The first axis, which accounted for most of the variability (28%), was highly correlated with the sea ice variables (sea ice concentration, minimum ice cover), which were inversely correlated with the presence of first year developmental stages. In contrast with *C. glacialis*, the centroids for the two periods were significantly offset, with the 2007–2016 period containing most of the stations with a high contribution of early life stages (C1–C3).

4 | DISCUSSION

When referring to *Calanus* in the Arctic, it is customary to separate the two species into the "shelf" or "neritic" *C. glacialis* and the "basin" or "oceanic" *C. hyperboreus* (Conover, 1988; Hirche, 1997; Jaschnov, 1970; Kosobokova, 2012). This paradigm, however, is facing increasing scrutiny (Choquet et al., 2017; Kvile et al., 2018), and our results

similarly suggest that the biogeography of the two *Calanus* species may be more complex than previously believed. Both species are found throughout the Arctic Ocean, and their core distribution (i.e., area where they can self-sustain their populations without advection from other regions) largely overlaps, centering on the outer shelf and slope of the Arctic Ocean. Furthermore, our results demonstrate that both species can inhabit waters with a wide range of bottom depths and that the observed trends in distribution of at least one of them, *C. glacialis*, is mainly driven not by bathymetry, but by sea ice dynamics. The abundances of *C. glacialis* decrease dramatically when moving away from the shelf break into the deeper basins, with the population of the latter mainly composed of later stage individuals, suggesting expatriation. The abundance of *C. hyperboreus*, on the other hand, is maintained also in the basins as a result of the accumulation of several previous generations (see detailed discussion below) (Figures 4c and 7b). The aforementioned dissimilarities in the distributions of the two species, which have led to the established classification of these two species into neritic/oceanic, reflect the differences in their life cycle traits such as annual routine, foraging behavior and body size (Conover, 1988; Falk-Petersen et al., 2009). These may result in uneven predation pressure (Berge et al., 2012) and a varying ability of the two species to withstand extended periods of starvation. The weak or absent correlations of abundance of later developmental stages to sea ice parameters in both species are expected, since these stages likely developed in previous years and can survive on lipid reserves (Hirche, 2013). Yet our results suggest that both species need extended periods of reduced sea ice concentration and open water to complete their life cycle: to reproduce, in the case of *C. glacialis*, or to reach their first overwintering stage, in the case of *C. hyperboreus*. These conditions are currently found only on the margins of the deep Arctic Ocean.

Calanus glacialis forms a distinct band of elevated biomass around the outer shelf and slope of the Arctic Ocean (Kosobokova, 2012; Kosobokova & Hirche, 2009; Wassmann et al., 2015). The shelf break, which was postulated to be a boundary for the horizontal distribution of this species, has historically coincided with the marginal ice zone, but this is now rapidly changing (Bluhm et al., 2020). Thus, it becomes important to distinguish that *C. glacialis* may not, in fact, be a shelf species within the Arctic, but rather a seasonal ice zone (SIZ)-associated species. Although the primary distribution area of *C. glacialis* is centered in the Arctic Ocean, self-sustaining populations are also present in sub-polar regions such as the White Sea (Pertsova & Kosobokova, 2003), Bering Sea (Nelson et al., 2009) and Sea of Okhotsk (Jaschnov, 1970), all of which notably have a pronounced seasonal ice cover. In the Bering Sea abundances of *C. glacialis* are strongly correlated with climate patterns, with colder, more ice-heavy years being characterized by higher biomass and higher lipid content of individuals (Banas et al., 2016; Eisner et al., 2018; Ershova et al., 2015; Kimmel et al., 2018). This suggests that this species thrives under an optimal ratio of open water—sea ice covered days over the course of a season, which is also indirectly supported by the general absence of this species in warmer regions. On the other hand, *C. glacialis* were also recently confirmed to be

present in a number of fjords in the Norwegian Sea (Choquet et al., 2018), many of which remain ice-free throughout the year, where they overlap in size and pigmentation with the co-occurring *C. finmarchicus*. The connectivity, life histories and specific adaptations that allow these populations to inhabit the fjord environment remain to be studied; yet they likely represent relict populations from the last glaciation event.

Although we did not directly measure reproduction in this study, the strong correlations of early life stage abundances of *C. glacialis* with periods of low sea ice and proximity to the ice edge suggest that ice retreat is the main factor triggering egg production and ensuring nauplial survival of this species. The question whether *C. glacialis* can also reach its overwintering stage and successfully overwinter in the deep basin, thus completing its life cycle, is outside of the scope of this work, but has been explored in modeling studies (Feng et al., 2016, 2018). Individual-based modeling of *C. glacialis* development controlled by food availability and temperature suggests that in conditions of reduced ice cover, the distribution of successfully overwintering *C. glacialis* significantly shifts polewards into the deep Arctic Basin. These shifts were particularly apparent when the modeled individuals were allowed to perform adaptive behavior, such as migrate to depth layers with abundant food. These models also did not include the possibility of feeding on microzooplankton, which has been shown to be a significant, and even preferred, part of *C. glacialis* diet in the Arctic (Campbell et al., 2009; Cleary et al., 2017) and potentially important to govern the annual life history events in Arctic *Calanus* (Hobbs et al., 2020). Deeper waters alone do not seem to be a hindrance for *C. glacialis* survival. Usually, their ontogenetic migration is restricted to the upper 300 m (Geynrikh et al., 1983; Kosobokova, 2012). However, they have been observed to also overwinter in deeper waters (Geynrikh et al., 1983; Kvile et al., 2019).

Although *C. hyperboreus* has been widely regarded an oceanic species resident to the deep Arctic Basins, recent evidence based on observations and modeling suggests that its core habitat is centered on lower-latitude regions, and most of the individuals observed in the basins are expatriates from the basins periphery (Kvile et al., 2018). Our results are in line with these conclusions; we similarly found the overall species abundance to be largely independent of bottom depth or distance to the shelf break. Although *C. hyperboreus* numbers are much higher than *C. glacialis* in the deeper basins, its absolute abundance and biomass there was often lower than on the outer shelf and slope. It is worth reiterating, however, that *C. hyperboreus* does largely dominate the zooplankton biomass in the oligotrophic central Arctic (Kosobokova, 2012; Kosobokova & Hirche, 2009), as very few other herbivorous plankton species can survive its harsh conditions. The latter fact may have historically reinforced the view that the central Arctic Ocean represents their core distribution area. It is noteworthy that *C. hyperboreus* employs a different reproductive strategy than *C. glacialis*, with adult females reproducing during the winter at depth, and the first few naupliar stages relying on lipid stores to grow. As such, spawning of this species is unaffected by immediate food availability. However, the distribution of early copepodite stages, and particularly the C3 stage, which is the first overwintering stage for this species, followed the same trends as the first year generation of *C. glacialis* (copepodite stages C1–C4), suggesting that despite the differences in the life history traits, similar processes control the distribution patterns of the two species. The only developmental stages of *C. hyperboreus* for which we observed a strong association with deeper oceanic regions were adult females and males.

The life expectancy of copepods is unknown, and *C. hyperboreus*, with its 3–4 year life cycle (Hirche, 1997, 2013), is probably among the longest lived among them. It is likely that the basins "accumulate" adults of this species, which are remarkably well adapted to long periods of starvation, perhaps over many consecutive years (Hirche, 2013). In the deep, ice-covered oligotrophic central basins of the Arctic Ocean, these large, less mobile individuals are more likely to survive as they do not become a target for predation, like they would in shallower, more productive peripheral waters of the Arctic Ocean containing many more pelagic predators (Kosobokova, 2012). However, as they cannot successfully complete their life cycle in these regions, the Arctic Basins will remain a zone of expatriation for *C. hyperboreus* unless they are carried by currents to more favorable regions.

There is an inherent challenge when trying to relate observational data to explanatory variables, as many among them can be correlated, and it can be difficult to discern the true driver versus a correlated one. Deeper areas away from the shelves in the Arctic coincide with the heaviest, thickest sea ice and the strongest seasonal light cycles. Furthermore, as neither of the two species is physically connected to the sea ice, the strong relationships to ice that we observe are reflective of yet other parameters, such as quality and quantity of primary production (e.g., Leu et al., 2015; Tedesco et al., 2019). The tight link between *C. glacialis* reproduction/life cycles and ice algal production has been documented (Leu et al., 2011; Runge & Ingram, 1988, 1991; Werner & Hirche, 2001) and also replicated in mechanistic modeling (Banas et al., 2016). Ice algae production is highest in thin, broken up ice (Tedesco et al., 2019). Additionally, recent evidence suggests that thinning of the sea ice could result in the proliferation of massive under-ice blooms (Arrigo et al., 2012; Assmy et al., 2017; Boles et al., 2020), which are not captured by satellite but can be a significant source of food for marine consumers. The strong correlations between the abundance of early life stages and ice characteristics suggest that *C. glacialis* rapidly and efficiently capitalizes on these events of ice thinning and ice retreat. For example, early stages of *C. glacialis* were observed in 2016 in the deep Amundsen Basin at 87°N, despite a 70%–80% ice cover at time of sampling. However, these stations experienced nearly 50 days of <50% ice cover, a number unprecedented at these high latitudes, which probably allowed ice algae to proliferate in these locations during the time of the species spawning. As the species can have different feeding preferences (e.g., there is direct evidence of *C. glacialis* feeding on ice algae (Runge & Ingram, 1991), but no such observations exist for

C. hyperboreus), changes in algal phenology may unevenly impact the two species, benefiting one more than the other. Rising sea temperature in the Arctic may also affect the two species differently, although the exact scope of those effects is difficult to predict. Both species have been observed to successfully survive in water temperatures up to 15°C and reproduce up to 8°C (Hirche, 1987; McLaren et al., 1969), although the temperature limit at which C. glacialis can maintain a positive metabolic balance
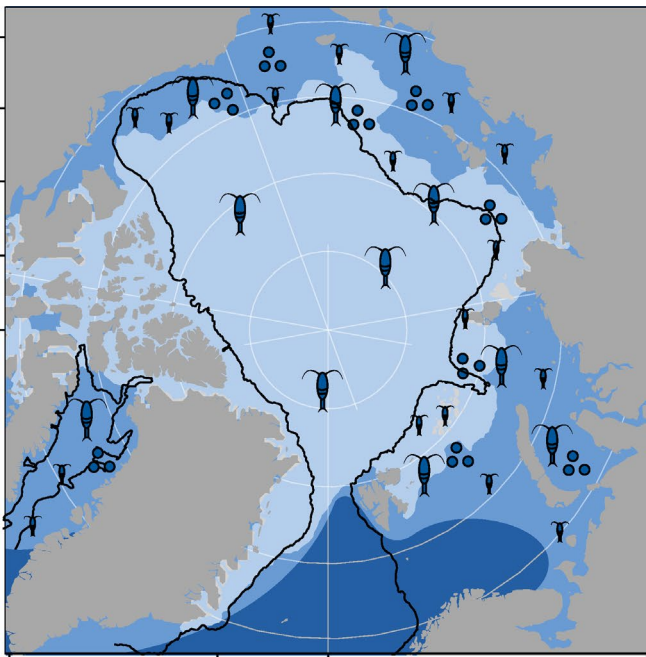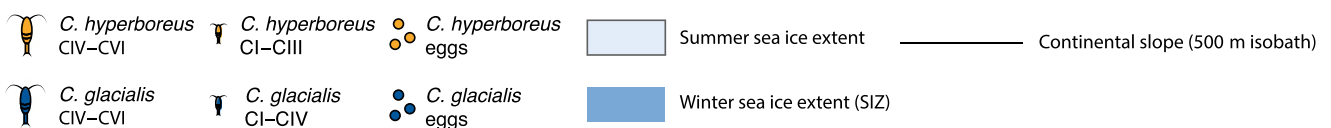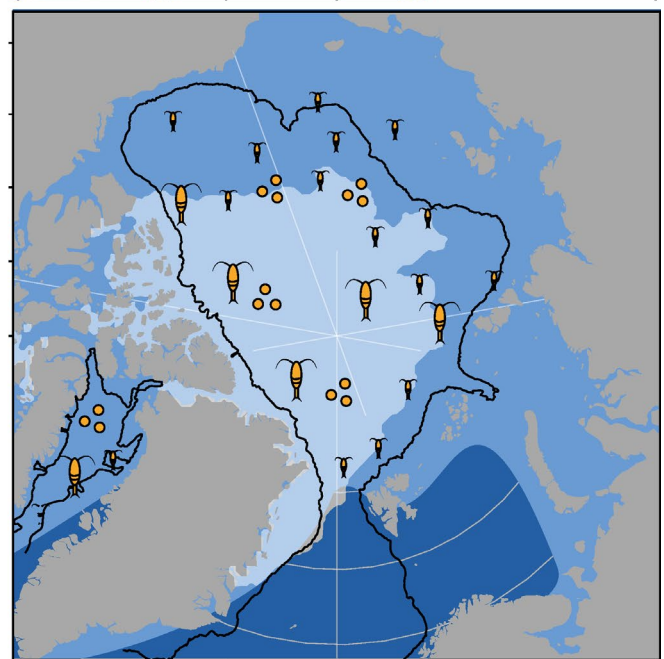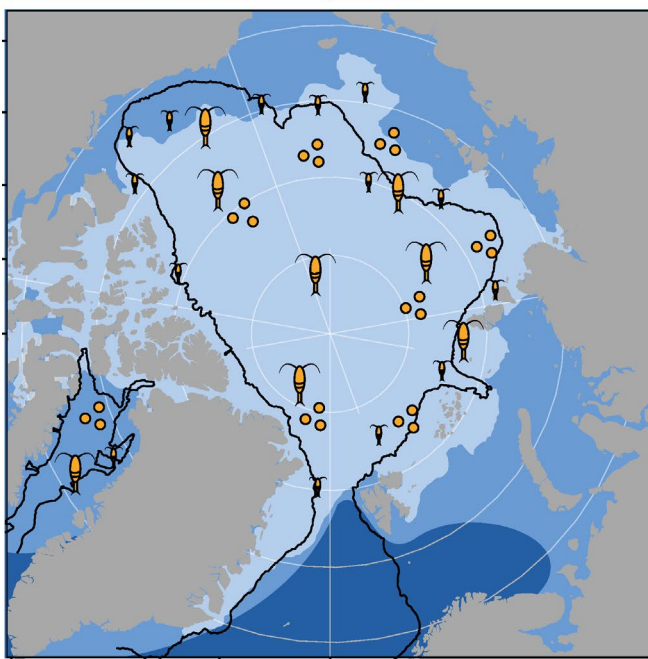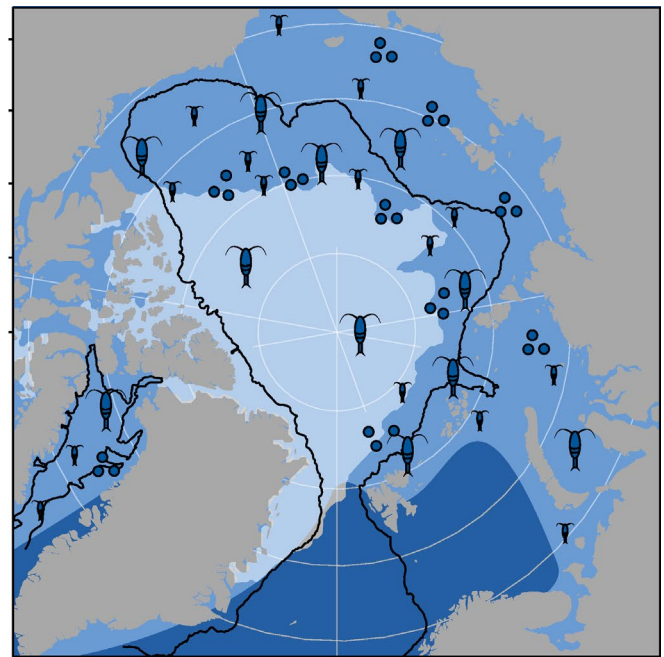

FIGURE 8 Conceptual model showing the present and future distributions of *Calanus glacialis* and *C. hyperboreus*, with a "typical" ice minimum (1993) and record low ice minimum (as observed in 2012). Late stages of *C. glacialis* are distributed throughout the Arctic Ocean, but reproduction only takes place in seasonally ice-covered waters. *C. hyperboreus* can reproduce under pack ice, but juveniles rely on ice-free waters to reach their first overwintering stage. Survival of this large, slow-growing species in shallower ice-free waters may be limited by competition and predation

is around 6°C (Alcaraz et al., 2014; Hildebrandt et al., 2014; Kosobokova, 1998). Counterintuitively, *C. hyperboreus* may be less sensitive to warming water temperatures, as it spends less time in surface waters, migrating to deeper layers earlier in the summer than *C. glacialis* (Darnis & Fortier, 2014).

Moreover, species distribution ranges are shaped not only by tolerance of physical environment. Ecological succession theory states that species with a higher tolerance for extreme conditions are often less competitive or may be more vulnerable to predation, and as conditions become less extreme, are replaced by more competitive species (Connell & Slatyer, 1977). The classical example in ecology is the rocky intertidal zone, where the upper ranges of the "bands" formed by the different organisms are shaped by the physiological tolerance to desiccation and fluctuations in temperature and salinity, whereas the lower extents are determined by competition or predation (Connell, 1961). This can present one explanation why we see *C. hyperboreus* advected northwards from its "core" range, but very little of the population survives southwards. If, as our results suggest, the life cycles and survival success of the two species are connected to sea ice dynamics, their ranges will continue to shift as the sea ice continues to retreat. As more and more of the Arctic Ocean becomes part of the seasonal ice zone, *C. glacialis* is expected to expand its range polewards. The range of *C. hyperboreus*, on the other hand, may contract farther into the basin, as this large, slow-growing species will be forced to compete with other zooplankton species or as visual pelagic predators follow the ice edge northwards (Figure 8).

5 | CONCLUSIONS

Our results support the increasing pool of evidence that the biogeographical constraints on the *Calanus* complex in the Arctic may be different than previously believed, and are more complex than the classic separation of *C. glacialis* and *C. hyperboreus* into the "shelf" and "basin" species. We conclude that the distribution centers of *C. glacialis* and *C. hyperboreus* in the Arctic largely overlap, and the two species can successfully inhabit waters with a wide range of bottom depths, with the different life history strategies and tolerance to long periods of starvation explaining the current dissimilarities in distribution patterns. The abundance of *C. glacialis* was highly correlated to sea ice parameters; although for *C. hyperboreus* the trends were weaker, they followed a similar pattern for early life stages, suggesting that both species need a period of reduced ice cover to complete their life cycle. Thus, we expect the distribution patterns of *Calanus* to continue to shift in the Arctic with retreating ice and changing climate conditions.

DATA AVAILABILITY STATEMENT
Data will be made available upon reasonable request to the corresponding author.

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SUPPORTING INFORMATION

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