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Abstract: Calanus spp. copepods play a key role in the Arctic pelagic ecosystem. Among four congeneric species of Calanus found in the Arctic Ocean and its marginal seas, two are expatriates in the Arctic (C. finmarchicus and C. marshallae) and two are endemic (C. glacialis and C. hyperboreus). The biogeography of these species likely is controlled by the interactions of their life history traits and physical environment. A mechanistic understanding of these interactions is critical to predicting their future responses to a warming environment. Using a 3-D individual-based model that incorporates temperature-dependent and, for some cases, food-dependent development rates, we show that 1) C. finmarchicus and C. marshallae are unable to penetrate, survive, and colonize the Arctic Ocean under present conditions of temperature, food availability, and length of the growth season, mainly due to insufficient time to reach their diapausing stage and slow transport of the copepods into the Arctic Ocean during the growing season or even during the following winter at the depths the copepods are believed to diapause. 2) For the two endemic species, the model suggests that their capability of diapausing at earlier copepodite stages and utilizing ice-algae as a food source (thus prolonging the growth season length) contribute to the population sustainability in the Arctic Ocean. 3) The inability of C. hyperboreus to attain their first diapause stage in the central Arctic, as demonstrated by the model, suggests that the central Arctic population may be advected from the surrounding shelf regions along with multi-year successive development and diapausing, and/or our current estimation of the growth parameters and the growth season length (based on empirical assessment or literature) needs to be further evaluated. Increasing the length of the growth season or increasing water temperature by 2°C, and therefore increasing development rates, greatly increased the area of the central Arctic in which the Arctic endemics could reach diapause but had little effect on the regions of successful diapause for the expatriate species.

Life history and biogeography of *Calanus* copepods in the Arctic Ocean: An individual-based modeling study

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Abstract: *Calanus spp.* copepods play a key role in the Arctic pelagic ecosystem. Among four congeneric species of *Calanus* found in the Arctic Ocean and its marginal seas, two are expatriates in the Arctic (*C. finmarchicus* and *C. marshallae*) and two are endemic (*C. glacialis* and *C. hyperboreus*). The biogeography of these species likely is controlled by the interactions of their life history traits and physical environment. A mechanistic understanding of these interactions is critical to predicting their future responses to a warming environment. Using a 3-D individual-based model that incorporates temperature-dependent and, for some cases, food-dependent development rates, we show that 1) *C. finmarchicus* and *C. marshallae* are unable to penetrate, survive, and colonize the Arctic Ocean under present conditions of temperature, food availability, and length of the growth season, mainly due to insufficient time to reach their diapausing stage and slow transport of the copepods into the Arctic Ocean during the growing season or even during the following winter at the depths the copepods are believed to diapause. 2) For the two endemic species, the model suggests that their capability of diapausing at earlier copepodite stages and utilizing ice-algae as a food source (thus prolonging the growth season length) contribute to the population sustainability in the Arctic Ocean. 3) The inability of *C. hyperboreus* to attain their first diapause stage in the central Arctic, as demonstrated by the model, suggests that the central Arctic population may be advected from the surrounding shelf regions along with multi-year successive development and diapausing, and/or our current estimation of the growth parameters and the growth season length (based on empirical assessment or literature) needs to be further evaluated. Increasing the length of the growth season or increasing water temperature by 2°C, and therefore increasing development rates, greatly increased the area of the central Arctic in which the Arctic endemics could reach diapause but had little effect on the regions of successful diapause for the expatriate species.

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1. Introduction

Copepods of the genus *Calanus* play a key role in arctic and sub-arctic pelagic ecosystems, usually dominating the biomass of the mesozooplankton in arctic and sub-arctic seas (e.g., Smith and Schnack-Schiel, 1990; Ashjian et al., 2003; Falk-Petersen et al., 2009). In the Barents Sea they can exert a significant impact on the primary production retaining much of the production in the pelagic food webs (Eilertsen et al., 1989; Hansen et al., 1990). However, when their biomass is low, as in the Chukchi, Beaufort, and Northern Bering Seas, most of the primary production is exported to the benthos because of insufficient grazing pressure (Grebmeier et al., 2006; Campbell et al., 2009). Due to their large body size and high lipid content, *Calanus* are an important high-quality food source for pelagic fish species such as capelin, herring, and pollock and can also be an important part of the diet for larval and juvenile demersal fishes (e.g. cod) (e.g., Wassman et al., 2006). Hence, the *Calanus* species are critical components of the carbon cycle on arctic and sub-arctic shelves and basins and dictate to a large degree the extent of pelagic-benthic coupling and the composition of the pelagic ecosystems.

Four congeneric species of *Calanus* are found in the Arctic Ocean and its marginal seas, two expatriates (*C. finmarchicus* and *C. marshallae*) and two endemics (*C. glacialis* and *C. hyperboreus*) (Conover, 1988; Smith and Schnack-Schiel, 1990). The literature on these species is extensive and cannot be comprehensive here. For the endemic species, *C. glacialis* dominates on the shelves and slopes while *C. hyperboreus* is most important in the deeper basin regions (e.g., Jaschnov, 1970; Conover, 1988; Hirche and Kwasniewski, 1997; Thibault et al., 1999; Kosobokova and Hirche, 2000, 2009; Ashjian et al., 2003; Wassman et al., 2006; Lane et al., 2007; Olli et al., 2007; Darnis et al., 2008;

Campbell et al., 2009; Falk-Petersen et al., 2009). Both these species can reproduce and grow in the extremely cold Arctic waters. The population centers of the expatriate species occur in more southerly waters. *C. finmarchicus* is advected into the Barents Sea from the Norwegian Sea and into the central Arctic through Fram Strait (Jaschnov, 1970; Conover, 1988; Hirche and Kosobokova, 2007; Falk-Petersen et al., 2009) and *C. marshallae*, if it does enter the Arctic, passes through Bering Strait from the northern Bering Sea (Frost 1974, Springer et al. 1989, Plourde et al. 2005; Hopcroft et al., 2010). Both these species are better adapted to warmer water conditions than those found in the Arctic Ocean proper.

The biogeography of copepods, as for many other ectothermic animal species in the ocean, is strongly affected by the temperature tolerance window to which they can adapt in order to sustain reproduction success and other life functions. Other environmental factors such as food availability can also be critical, as well as the life history traits of organisms including development and reproduction strategies under certain temperature and food conditions and the timing of these traits relative to seasonality of the environment (phenology). In the Arctic Ocean, low temperatures and the resulting slow growth and development rates have resulted in multi-year life cycles for the endemic *Calanus* spp. (e.g., Conover, 1988; Smith and Schnack-Schiel, 1990; Madsen et al, 2001; Falk-Petersen et al., 2009). The *Calanus* spp. are omnivores, utilizing phytoplankton, microzooplankton, and, in the Arctic, ice algae as food (e.g., Barthel, 1988, 1990; Stoecker and Capuzzo, 1990; Campbell et al., 2009). In arctic and subarctic waters, the species reproduce during periods of food availability and mature through the productive season to a diapausing stage at which they overwinter, generally at depth below the euphotic zone and/or permanent thermocline (e.g., Falk-Petersen et al., 2009). *Calanus hyperboreus* is generally believed to require three years for maturation, while *C. glacialis* requires two years with exceptions observed at some locations such as the Canadian Archipelago. In warmer, temperate regions, *C. finmarchicus* and *C. marshallae* can mature within months and produce several generations in a single productive season while in colder regions a year including an overwintering in diapause is required for maturation (e.g., Madsen et al., 2001). All four species store lipid during the productive season on which they depend during overwintering, with at least one (*C. hyperboreus*) also utilizing those lipid reserves to support reproduction. In the central Arctic, *C. hyperboreus* produces eggs at depth prior to the growing season entirely from lipid reserves accumulated during the previous year, with the result that the first feeding stage (N3) is ready to take advantage of the ice/water column production as soon as it begins (Ashjian et al., 2003; Ashjian and Campbell personal observations). Based on gonad development state observations and early season egg production experiments, *C. glacialis* also may utilized stored lipid for reproduction prior to the spring bloom although most of their reproduction is food dependent and occurs during periods when phytoplankton and microzooplankton food are available (Smith, 1990; Hirche and Kattner, 1993; Kosobokova, 1999; Niehoff et al., 2002; Hirche and Kosobokova, 2003). To complete a life cycle in the Arctic Ocean it is necessary that individuals reach a life stage where diapause can be initiated and store sufficient lipid at that stage for overwintering before the end of the productive season when food availability is diminished. Therefore, species such as *C. finmarchicus* may not be able to colonize the Arctic Ocean, simply because their development rates in low-temperature and low-food environments are too slow to attain their overwintering stage and to store sufficient lipid. These dynamics could be altered as the environmental conditions change (e.g. warming and earlier snow/ice melting) in the Arctic and marginal seas.

The Arctic is particularly susceptible to climate warming, seen most clearly in the recent seasonal ice retreat in the western Arctic (Serreze et al., 2007; Stroeve et al., 2007). It has been predicted that seasonal ice cover in the central Arctic could essentially disappear by ~2030 (Stroeve et al., 2008; Markus et al., 2009; Wang and Overland, 2009). Warming ocean temperatures, decreasing seasonal ice cover, and thinning sea ice with greater development of leads and small polynyas (e.g., Lindsay and Zhang, 2005; Giles et al., 2008; Markus et al., 2009) could increase the phytoplankton growth season and thus the total primary production. This change in production levels and seasonality could provide better growth conditions and a longer growth season for *C. finmarchicus*, making it possible for this species to expand its range from the northern North Atlantic further into the Arctic and its marginal seas. Endemic species, such as *C. glacialis* that may rely on ice algae to fuel reproduction at the beginning of their growth season, could be negatively impacted due to the loss of the sea ice and associated algae production. A change in the *Calanus* species composition might cause a regime shift of ecosystem structure and function in the Arctic Ocean. Such a shift has been observed in the North Sea, where changes in plankton composition, primarily a shift in the abundance dominant from *C. finmarchicus* to its warmer water congener *C. helgolandicus*, along with a shift in the timing of peak *Calanus* biomass, has led through bottom up control to long-term changes in Atlantic cod recruitment (Beaugrand et al., 2003).

It is essential to understand how the combination of life history traits, development rates, physical advection, seasonality, and the food environment limits and maintains the ranges of *Calanus spp.* populations before an understanding of how climate change might shift *Calanus* spp. biogeographic boundaries in the Arctic Ocean and marginal seas can be achieved. The multiple processes involved in controlling the biogeography and the limited observational data available for detailed analysis make this challenging. Here, the factors that control *Calanus* spp. population dynamics and biogeographic boundaries in the Arctic Ocean and marginal seas are explored using a biological-physical coupled model. Two overarching questions are considered: 1) What determines the present biogeographic boundaries of the four *Calanus* species? and 2) How might the present biogeographic boundaries and distributions change under projected future climate warming? Specific hypotheses that are explored include: 1) Successful recruitment and persistence of populations of the different species are dependent on water temperature and the length of the growth season; 2) The distributions of the different species are dictated by their ability to recruit and persist at the ambient environmental conditions of each location to which they are advected and 3) Lengthening the growth season and/or increasing water temperature, possible results of climate change, can expand the range of the different species because successful colonization and recruitment can occur at previously inhospitable locations.

2. Material and methods

The general approach of the study was to couple a copepod individual-based model (IBM) to a realistic physical ocean model. Starting locations that were coupled to model nodes were identified for each of the four *Calanus* spp. At each location, a model copepod was permitted to develop based on temperature and, in some cases, food dependent development rates. The model copepod at each location was advected according to the model circulation and developed from the start until the end of the copepod growth season. The length of the copepod growth season for each location was based on the period over which chlorophyll food was available; this period is referred to herein as the growth season. The start/end dates of the copepod growth season and the daily water temperature and food concentration were location dependent and were calculated for each point at each model time step. At the end of the growth season, the life stage achieved was assessed to determine if the copepod had reached a stage and estimated lipid storage level at which it could diapause. The locations of individuals that succeeded were plotted geographically to identify locations and regions likely to be occupied, or potentially colonized, by each species. A set of different environmental scenarios, including present temperature and growth season length, elevated temperature, and longer growth season were run to explore sensitivity of the results to such changes and to explore the potential impact of future climate change on the species' ability to expand their distributions.

2.1. Physical model

The physical ice-ocean model was an updated version of the Arctic Ocean Finite-Volume Community Ocean Model (AO-FVCOM) (Chen et al., 2009) that is based on the spherical coordinate, semi-implicit version of the Finite-Volume Community Ocean Model (FVCOM) fully coupled to an Unstructured Grid version of the Los Alamos sea ice model Community Ice CodE (UG-CICE) (Chen et al., 2003; Hunke and Lipscomb, 2006; Gao et al., 2010). The computational domain covers the Pan-Arctic region (Fig. 1). A non-overlapped triangular grid is used in the horizontal and a hybrid coordinate in the vertical. The horizontal resolution varies over 10-50 km and the vertical resolution depends on water depth. The water column has a total of 45 layers. In regions deeper than 225 m, the s-coordinate is chosen with ten and five uniform layers of 5 m thickness specified near the surface and bottom, respectively, with uniform depths of thickness depending on water depth between the surface and bottom layers. In shelf regions of ≤ 225 m water depth, the σ-coordinate is used with a uniform vertical resolution of 5 m or less throughout the water column and thickness depending on water depth. These two coordinate systems merge at the 225-m isobath, where all layers have a uniform thickness of 5 m. The time step used to drive AO-FVCOM was 600 seconds. The ice internal stress in UG-CICE was updated using 120 sub-iterations at a time step of 5 seconds.

The AO-FVCOM model was driven by 1) astronomic tidal forcing constructed from eight tidal constituents (M_2, S_2, N_2, K_2, K_1, P_1, O_1 and Q_1), 2) the surface wind stress, 3) the net heat flux at the surface plus shortwave irradiance in the water column, 4) the air pressure gradient, 5) precipitation minus evaporation, and 6) river discharge. The meteorological forcing data were climatologically averaged fields over 1978-1994 derived from the ECMWF reanalysis ERA-15 from the database (version 6) of the Arctic Ocean Modeling Intercomparison Project (AOMIP). River discharge along the US and Canada coast was specified by the daily climatologic mean from USGS monitoring sites (http://www.usgs.gov and www.ec.gc.ca) while data outside the US and Canada coast was provided by L. F. Smedstad at the Navy Coastal Ocean Modeling (NCOM) Group.

The AO-FVCOM was nested in the Global-FVCOM, which provides the surface elevation, currents, water temperature/salinity and mixing coefficients at the open boundaries. The Global-FVCOM was spun up for a 50-year run, while AO-FVCOM runs were initialized with the Global-FVCOM spin-up field and ran for 6 years with data assimilation of monthly climatologic temperature and salinity fields. The model-predicted fields reached an equilibrium state after 5 years, and the selected integration time was long enough to conduct the climatologic field used for this study.

2.2. Biological model

2.2.1: General framework

An FVCOM-based IBM was implemented with two modules, a Lagrangian tracking module and a generic life stage-based biological module. The tracking module is driven by the velocity fields derived from the hourly-archived FVCOM output (so-called "offline" approach). The resulting locations of individual particles, along with the temperature field from FVCOM, provided input for the biological module.

In the Lagrangian tracking module, the movement of each individual particle by advection (and possibly vertical migration) was computed by solving the following equation with a classic 4th order 4-stage explicit Runge-Kutta method implemented in FVCOM (Chen et al., 2006; Huret et al., 2007), $d\vec{x}/dt = \vec{v}(\vec{x}(t), t) + \overrightarrow{v_b}$, where $\vec{x}$ was the particle position at time t, and $\vec{v}$ was the velocity interpolated from the surrounding model grids provided by FVCOM. The biological behavior term $\overrightarrow{v_b}$ can be derived from the literature/field measurements. In this study, swimming behavior was not included and individual particles/copepods were maintained at specific depths (e.g. 0 m or 50 m during the growth season, and 200 m during diapause) during the model runs.

In the biological module, the entire life cycle of the target zooplankton species was divided into 13 distinct stages including egg, nauplii (6 stages), and copepodid (6 stages), which includes the adult. An individual copepod was represented as a vector in the model with information such as location (*x*,*y*,*z*), age and stage (referred to as *i*-state by Metz and Diekmann, 1986). Each vector was updated at each time step according to development rate and reproductive functions derived from field measurements and lab experiments. The model started with an initial development stage and spatial distribution, then monitored the change of each individual by recording the *i*-state of individual *j* at any time *t* (Miller et al., 1998; Carlotti et al., 2000):

$$X_{i,j}(t) = X_{i,j}(t - dt) + f(x_{1,j}(t - dt), ... x_{i,j}(t - dt), ..., T, food, ...), \qquad (1)$$

where $X_{i,j}(t)$ was the value of the *i*-state of individual *j*, and *f* was the process modifying $X_{i,j}$ as a function of the values of different *i*-states of the organism and external parameters such as the temperature *T* and food concentration.

2.2.2. Development rate parameterization

Belehrádek's (1935) temperature function was used to describe the development times under saturated food conditions as a function of temperature following Corkett et al. (1986). Development time (D) for any one given stage was given by

$$D = a(T + \alpha)^{\beta}, \qquad (2)$$

where a, α and β are fitted constants and T is temperature. The value β was taken to be −2.05 from Corkett et al. (1986), who found this to be the mean for 11 species of copepods. The parameters for *C. finmarchicus* were taken from a laboratory rearing study at 4, 8, and 12 °C by Campbell et al. (2001). For *C. glacialis* and *C. hyperboreus*, the remaining parameters were determined by fitting the equation to egg development times. For *C. glacialis*, the egg development time function derived by Corkett et al. (1986) from data collected at 2 to 10 °C was used and verified with egg hatching times collected at 0°C (Campbell and Ashjian unpub.). For *C. hyperboreus* a function for egg development time was fit with data from experiments conducted at 0 to 8 °C by Corkett et al. (1986) and at -1 °C by Campbell and Ashjian (unpub.). The value for α was then taken to be constant over the entire life span of a species. For *C. finmarchicus*, *C. glacialis* and *C. hyperboreus*, α is equal to 9.11, 13.04 and 13.66, respectively. The value for a, which determines the stage-specific component of development time, was determined for the remaining stages based on the intra-generic equiproportional rule for copepod development (Hart 1990): namely that the proportion of time that an individual spends in a given stage relative to the entire development time is constant across genera and across different temperatures. This permitted the coupling of stage-duration proportions determined for *C. finmarchicus* (Campbell et al., 2001) with the egg development time functions from the other *Calanus* species to derive stage specific development times (determined by a) at different temperatures for each species of interest. Arnkvaern et al. (2005) computed the stage durations for these three species using the same data set from Corkett et al. (1986) and Campbell et al. (2001) and showed similar results to ours. We attempted to use egg-hatching times for *C. marshallae* from Peterson (1986) to derive a similar function for this species. However, the temperature range was too high and narrow (9 to 12°C), and despite having very similar egg development rates to those of *C. finmarchicus* and *C. glacialis* at those temperatures, the response to temperature was very flat with the result that the derived function gave unrealistically fast development rates when extrapolated to cold temperatures. In addition, we compared the estimates of *C. marshallae* generation times from the laboratory studies of Peterson (1986) and the field-determined copepodid stage durations from Liu and Hopcroft (2007) and found that they were on the order of 1.5 to 2 times longer than the equivalent stages for *C. finmarchicus* and *C. glacialis*. We concluded that these were not likely the maximum development rates for this species and decided to use the temperature functions for *C. finmarchicus*, which inhabits a similar temperature environment, to provide an optimal case scenario for the invasion of *C. marshallae* into the Arctic. The daily temperature distribution was derived from the FVCOM model output.

The life-stage specific dependence of development rate on temperature was computed from the Belehrádek's functions (parameters in Table 1) for *C. finmarchicus, C. glacialis,* and *C. hyperboreus* (Fig. 2). Development time from egg to C1 and from egg to adult for *C. hyperboreus* is longer than for *C. glacialis* (Figs. 2d, e), consistent with a 2-year life cycle for *C. glacialis* and a 3-year life cycle for *C. hyperboreus.* For *C. finmarchicus*, these development times are shorter (on the order days) at warmer temperatures (8-10 °C) but become equivalent to or longer at lower temperatures than for the Arctic endemics. The "critical development time" is that from the stage first requiring food to the first diapausing stage (Fig. 2f), since this must be accomplished within the growth season. We use the predominate stage of first diapause observed in field collections for each species; younger stages have been observed to enter diapause, but may have much lower survival. *C. finmarchicus*, *C. glacialis* and *C. marshallae* require food for significant reproduction by the females (Madsen et al, 2001); while *C. hyperboreus* need food at the first feeding nauplius stage (N3) since egg production is fueled by lipid reserves and the

N3 stage is present in the water column prior to the start of the growth season (Ashjian et al., 2003). These different reproduction strategies are also known as income-breeder (food-dependent reproduction) and capital-breeder (lipid-based reproduction) (Varpe et al., 2009). Differences in these times between species can be accounted for by the different life history strategies of each. Much longer critical development times were calculated for *C. finmarchicus* that first requires food at egg production, diapauses at a mature copepodid stage (C5), and that has longer development times at lower temperatures than for the Arctic endemics, suggesting that *C. finmarchicus* is not well adapted to develop at cold temperatures. Critical development times for *C. glacialis* were longer than for *C. hyperboreus* at Arctic temperatures (10 days longer at -1.8 °C, 6 days longer at 0°C), despite C. *hyperboreus* requiring longer time overall to develop (Fig. 2e), because *C. glacialis* requires food at egg production rather than at the first feeding nauplius stage (N3; *C. hyperboreus*) and diapauses at an older copepodid stage (C4) than *C. hyperboreus* (C3). Critical development times become more similar for Arctic endemics at ~5°C and start to converge for the three species at >10°C.

In addition to temperature, food dependence was added to the development rate equations of *C. finmarchicus* and *C marshallae* for further simulations, using a similar approach to Speirs et al. (2005), who fit the function to the observation data from Campbell et al. (2001). The development duration (D) becomes

$$D = a(T+\alpha)^{\beta} / \left[1 - \exp\left(-{}^{F}\!/_{K}\right)\right], \tag{3}$$

where *F* is food concentration (unit: μg chl l^{-1}), and *K* was a constant associated with the intensity of food limitation (0.8 μg chl l^{-1} in this model, derived from Campbell et al., 2001). No experiments with food-dependent development were conducted for the Arctic endemics *C. glacialis* and *C. hyperboreus,* due to difficulty in estimating food concentration (ice algae data is very sparse; phytoplankton in ice-covered seas cannot be detected from satellites).

2.2.3. Growth season estimation and starting locations for simulations

The copepod growth season was assumed to be equivalent to the period of time during which food, represented here by phytoplankton availability, was available. Copepod growth based on grazing on microzooplankton also is likely important (e.g. Campbell et al. 2009), however this was not included specifically in the model. In general, microzooplankton do not become abundant until sufficient phytoplankton food is available to support microzooplankton growth (Sherr et al., 2009) so availability of phytoplankton can serve as a proxy for overall food availability for *Calanus* spp. Food concentration and the specific lengths of the primary production season were derived for each location from two different sources, with those further north necessarily having shorter growth seasons. For locations that were only seasonally ice covered, a climatology (from 1998-2007) of 8-day composites of SeaWiFS chlorophyll *a* data were used to estimate the dates that food was first and last available, as when the chlorophyll *a* is higher than the satellite detection limit (0.01 mg Chl-*a* m^{-3}) at each grid point in the IBM modeled field. The growth season was considered to have ended when chlorophyll concentration once again below the satellite detection limit in the fall. This method was used for simulations with the two expatriate species only. Locations that are perennially ice covered, such as in the central Arctic, do not have SeaWiFS chlorophyll *a* data available and hence the growth season was computed for each ice covered location using satellite-derived snow melt onset data (Drobot and Anderson, 2001, updated 2009) to estimate the start date and FVCOM-computed sea surface short-wave radiation to estimate the end date (growth season ended at irradiance < 20 W/m^2). This method was used for all simulations with the endemic species and one simulation with the expatriate species. It is possible that primary production, particularly of ice algae, commenced prior to the date of complete snow melt, particularly in regions where melt ponds were common on the ice or where leads developed between ice floes, however a reliable method of predicting the timing of this earlier production was not available. At locations in the marginal ice zones where both satellite chlorophyll *a* data and satellite snow melt data were available, the latter were used to determine the start of the growth season since production commences under sea ice once snow melts but will not be detected as ocean color by satellites prior to ice melt. Food concentrations were estimated for each date and location where SeaWiFS chlorophyll *a* data from the climatology were available.

The beginning of the copepod growth season was used to set the onset of egg production at each of the model node points for *C. finmarchicus, C. marshallae,* and *C. glacialis*, under the assumption that food was required to fuel significant reproduction (e.g., Conover, 1988; Smith and Schnack-Schiel, 1990; Falk-Petersen et al., 2009). For *C. hyperboreus*, the presence of the first feeding nauplius stage N3 was set to coincide with the onset of the copepod growth season. The starting grid points for most simulations with *C. finmarchicus* and *C. marshallae* were all locations where chlorophyll *a* data were available from satellite (Fig. 3). By contrast, the starting grid points for the Arctic species *C. glacialis* and *C. hyperboreus*, and for one simulation with the expatriate species, were all locations where the onset of snow melt was used to determine the growth season; this would include all locations in the central Arctic. Although *C. glacialis* and *C hyperboreus* are found further to the south than these locations, the present study focused on factors determining the geographic distributions of the copepod species within the Arctic Ocean. The growth season starts earlier at locations of known polynyas such as the Amundsen Gulf, the northern end of Baffin Bay (North Water Polynya), and the northeast corner of Greenland (Northeast Water Polynya) than at other locations at similar latitudes. Reproduction in *Calanus* spp. certainly is not limited to the start of the productive season and can continue for several months after that date, however those individuals would experience a shorter growth season because the end of the productive season remains fixed. Hence, the simulations presented here represent the maximum growth during one feeding season.

2.2.4. Tracking and evaluation

Once an individual was released, it was advected by the dominant circulation and developed from node to node according to the temperature at each point and, for some simulations and locations, the food concentration. The model permitted simulation of development and movement of individuals at different depths, each of which experienced different temperature conditions. Development was terminated when the individual reached a location-specific date where food was no longer available. Development was deemed to be successful if an individual had advanced halfway into a life stage at the end of the growth season where diapause can be initiated, with Copepodid Stage 5 (C5) for *C. finmarchicus* (e.g. Hirche, 1990), C3 or *C. hyperboreus* (e.g., Ashjian et al. 2003), and C4 for *glacialis* (e.g., Falk-Petersen et al., 2009). The requirement to develop past the inception of the diapausing stage permits sufficient accumulation of lipid to occur to support overwintering.

2.3. Numerical experiments

A series of numerical experiments were conducted to test the proposed hypotheses regarding the geographic ranges of *Calanus* spp. populations and how temperature- and food-dependent development rates coupled with advection by the prevailing circulation might dictate their distributions (Table 2). For *C. finmarchicus* and *C. marshallae*, simulations were conducted for the duration of the growth season as 1) temperature-dependent development only with individuals at both 0 m and at 50 m and (2) both temperature- and food-dependent development at both 0 m and 50 m. A single simulation was done with temperature dependent development only, advection at 0 m, and using the snowmelt proxy for the growth season with starting locations covering the entire Arctic region (Fig. 3) to determine if these species could reach diapause over this broader area. For *C. glacialis* and *C. hyperboreus*, simulations were conducted for the duration of the growth season as defined using snowmelt (Fig. 3) at 0 m and at 50 m using temperature-dependent development rates only because food concentration was unavailable for the central Arctic.

To test the effect that early, lipid-based reproduction might have on the recruitment success of C. *glacialis* in the central Arctic, a simulation was conducted starting *C. glacialis* at stage N3, which would be the first feeding stage for lipid based reproduction, at the start of the growth season, advected at 0 m, under temperature dependent development only, and using snow melt/irradiance to define the growth season.

Most simulations followed individuals only for one growth season to identify the locations of each individual that successfully achieves the diapause state. The logic behind this is that failure to reach diapause can be considered a failure to survive and reproduce. Further advection, potentially into the central Arctic, during overwintering and diapause and after the end of the productive season was investigated by advecting successfully diapausing copepods at depth through the winter. For *C. finmarchicus* and *C. marshallae*, the model run stopped at the 2nd year, whereas for *C. glacialis* and *C. hyperboreus*, the model ran continuously (active development at surface during the growth season, and diapause at depth during non-growth season) through the 3rd and 4th year, respectively. These individuals presumably then would be able to continue development to the next overwintering stage or to the adult stage and reproduce. Diapausing individuals were tracked at 200 m at each grid point where the bottom depth was > 200 m or at 5 m off the bottom where the bottom depth was 200 m or less. Although 200 m is at the believed upper portion of the diapausing depth range, this represented a best-case scenario for transport since velocities diminish rapidly at greater depths.

Because of the difficulty in predicting the start of the productive season (and hence the length of the copepod growth season) in the central Arctic, a simulation was conducted in which the start of the growth season was set to be two weeks earlier than predicted based on snow melt/irradiance alone to explore the success of each species if food is actually available earlier (e.g., production before snow melt) and to test the effect of an earlier and longer growth season under climate change.

The potential impact of warming on copepod development and successful recruitment to the diapausing stage was investigated by increasing the water temperature 2 °C over the climatological temperature for each node point in the model. Development and advection of *C. finmarchicus* and *C. marshallae* (temperature and food-dependent development) and of *C. hyperboreus* and *C. glacialis* (temperature-dependent development) at the surface (0 m) then were tracked as for the other simulations. Only water temperature was changed for these simulations; no changes in ice coverage, food concentration, and length of the productive season that might accompany an increase in water temperature were included.

For the two expatriate species, a simulation at the surface in which both temperature was increased by 2°C and the growth season was set start two weeks earlier also was done to explore the impact of changing both of these conditions.

3. Results

3.1. Physical Model

Cimatological fields of the sea ice coverage and concentration, water temperature, salinity and currents simulated by the ice-ocean model AO-FVCOM have been validated by comparison with observational data from satellites, mooring, drifters/floats and climatologically averaged hydrographic database (Gao et al., 2010; Chen et al., 2010). The model captured the spatial distribution and seasonal variation of both sea ice and currents in the Arctic and adjacent regions. To focus our discussion on the biological modeling results, we only include a brief description of physical model results here.

In early spring, the surface circulation in the central Arctic is characterized by a well-developed anti-cyclonic Beaufort Gyre and a strong Transpolar Drift current extending from Russia across the central Arctic to NE Greenland (Fig. 4). Sea surface temperature is nearly constant across the central Arctic. The influence of inflowing warmer Atlantic water is seen in the elevated sea surface temperatures along the coast of Norway while outflowing Arctic water is seen as the very cold water extending to the south along the eastern coast of Greenland. In summer, elevated sea surface temperatures are seen on all of margins of the central Arctic, on the continental shelves, with the exception of the region just to the north of Greenland and the Canadian Archipelago where substantial multi-year sea ice has been observed recurrently (e.g. Walsh and Zwally, 1990). The anti-cyclonic Beaufort Gyre shrinks and is much weaker and also the Transpolar Drift shifts toward North American side of the central Arctic. Coastal currents can reach 20-30 cm/s in September but are as low as 10 cm/s in April. Transport through Bering Strait for these two months are ~1.4 Sv and 0.6 Sv, respectively, which are close to long term mooring observations of 1.2 Sv and 0.6 Sv in summer and winter (Woodgate et al, 2005). The net inflow into the Arctic Ocean through the Fram Strait is ~1.6 Sv, which balances the outflow along the Greenland shelf. The model-predicted northward current west of Spitsbergen is about 10-20 cm/s, close to observations (Fahrbach et al., 2001). The temperature in Fram Strait is as high as 6-8 °C in September and as low to 1-3°C in April.

3.2. Biological Simulations

Since the same temperature and food dependent development rates were used for both *C. marshallae* and *C. finmarchicus*, in presenting results their development and advection were combined over the entire central Arctic as a single plot; *C. finmarchicus* is presented on the Atlantic side and *C. marshallae* is presented on the Pacific side. There was no overlap of advected individuals between the Pacific (*C. marshallae*) and Atlantic (*C. finmarchicus*) sides of the Arctic for all simulations. Under development rates that are temperature-dependent only, with the copepods at the surface and using both criteria to define the length of the growth season, *C. finmarchicus* was able to successfully reach the diapausing stage of C5 only in the Barents, southern Kara and southern GIN Seas and at a few locations in Baffin Bay (Fig. 5, Atlantic side), with no penetration of the species into the central Arctic. Even the copepods that failed to reach diapause were not advected into the central Arctic by the end of the growth season (trajectories not shown). If development rate is also food limited, *C. finmarchicus* successfully reaches diapause only at locations considerably further south in the GIN and Barents Seas and in the Spitzbergen Current (Fig. 6).

The *C. finmarchicus* individuals released and advected at 50 m, under temperature-dependent only development rate, were not able to reach diapause at locations as far north in the Barents Sea as those at the surface (not shown here). Under both food and temperature dependent development rates at 50 m, successful diapause was achieved only in the southern portions of the GIN and Barents Seas and in the warm Atlantic water running north along the western side of Spitzbergen (Fig. 6). Some eastward advection of successfully developing copepods along the shelf-break to the north of Spitzbergen did occur.

For *C. marshallae*, if the development is temperature-dependent only, surface individuals released in the Bering Strait and on the Chukchi-Beaufort shelf were able to successfully reach C5 only along the Chukchi and Beaufort Shelf breaks and at a few locations in Amundsen Gulf (Fig. 5, Pacific side). Under the development rate that depends on both temperature and food, very few surface individuals can reach C5 within the growth season in the Chukchi-Beaufort shelf region (Fig. 6), and no individuals reached C5 if individuals stayed at 50 m below the surface (Fig. 6).

Both *C. glacialis* and *C. hyperboreus* could not reach even their earliest diapause stages (C4 and C3, respectively) in the central Arctic (even without including food limitation on development in the simulations) when the growth season starts at the onset of snow melt both at the surface (Fig. 7) and at 50 m (not shown, distribution similar to that at the surface). Successful *C. glacialis* were distributed along the edges of the central Arctic and in the marginal seas, except for the highly advective Chukchi and western Greenland Seas where most *C. glacialis* were advected out of the region by the end of the growth season. Successful *C. hyperboreus* also were distributed in the marginal seas (except for the Chukchi and western Greenland Seas) and in the Canadian Archipelago as well as in the Beaufort Gyre and along the northern edges of the Chukchi Borderland. The distribution of successful *C. hyperboreus* extended further into the central Arctic than did *C. glacialis*, due to the shorter critical growth period of *C. hyperboreus* that permitted diapause to be reached in a shorter period of time. The distribution of successful *C. glacialis* from the simulation in which *C. glacialis* was assumed to reproduce prior to the spring bloom based on lipid (not shown) extended further northward than that resulting from food-dependent reproduction (Fig. 7a) and was very similar to the distribution of successful *C. hyperboreus* under the same environmental conditions (Fig. 7b). Both species were observed in the Arctic boundary current that advects Atlantic water to the east along the continental shelf north of Spitzbergen (Rudels et al., 2000).

Advection of diapausing individuals at depth during the overwintering period demonstrated that the extent and distribution of diapausing copepods being advected further into the Arctic Ocean, varies with different species (Fig. 8). *C. finmarchicus* was advected further into the central Arctic in the northward extension of the Spitzbergen Current and occupied more of the Barents Sea, but showed no signs of crossing the central Arctic. *C. marshallae* was advected further to the north along the northern edge of the Archipelago. Both *C. glacialis* and *C. hyperboreus* extended their ranges deep into the central Arctic, especially in the north of the Laptev Sea in the Transpolar Drift. Overall, the increase in spatial coverage during overwintering advection for *C. finmarchicus* and *C. marshallae* was not significant, but for *C. glacialis* and *C. hyperboreus,* the multi-year successive development and overwintering advection could potentially contribute to the maintenance of a central Arctic population.

Increasing the length of the growth season by two weeks had a noticeable impact on the distributions of locations where the Arctic endemics could reach diapause but had little effect on those distributions for the Arctic expatriates (Fig. 9). In particular, *C. hyperboreus* successfully achieved diapause at all locations in the central Arctic with the exception of the area to the north of Greenland and the Canadian Archipelago (in contrast to the simulation with the shorter growth season where the copepod could not achieve diapause in the central Arctic). The distribution of successful diapause locations for *C. glacialis* was extended somewhat into the central Arctic, particularly in the Beaufort Sea, however the effect was not large. The longer growth season did not appreciably extend the distribution of locations where *C. finmarchicus* and *C. glacialis* could reach diapause.

An increase of 2°C in the ambient water temperature did not substantially change the distributions of the Arctic expatriates *C. finmarchicus* and *C. marshallae* that successfully reached diapause (Fig. 10). By contrast, the warmer temperatures dramatically increased the regions over which the Arctic endemics *C. hyperboreus* and *C. glacialis* were able to reach diapause, with successful recruitment of *C. hyperboreus* over the entire and *C. glacialis* over much, but not all, of the central Arctic. Starting the growth season earlier in addition to increasing temperature did not substantially expand the distribution of where the expatriate species were able to achieve diapause.

Note that because there are no inputs in the model from outside the central Arctic, there will be locations from where water and copepods were advected during the simulations for which there will be no replacement.

4. Discussion

The modeling simulations demonstrated that the observed biogeographic distributions of the four *Calanus* species is consistent with the distributions modeled by coupling the life history characteristics and development rates of the individual species to water temperature, to the duration of when food is available to the copepods, and to the prevailing velocity and direction of circulation. Both expatriate species *C. finmarchicus* and *C. marshallae* are unlikely under present environmental conditions to colonize the central Arctic proper because the length of the growth season there is too short to permit development of progeny to the diapausing stage at which successful overwintering, and reproduction the following year, can occur. By contrast, both endemic species *C. glacialis* and *C. hyperboreus* are far more successful in the marginal seas and the central Arctic and can maintain viable populations in those regions. Only the Arctic endemic species responded to increased water temperature or a lengthening of the growth season by increasing the range of locations in the central Arctic where successful recruitment to diapause could occur.

Arctic Endemics – C. glacialis and C. hyperboreus

Both *C. glacialis* and *C. hyperboreus* were successful in marginal seas and along the slope of the central Arctic under temperature dependent growth only. The simulations were unable to include the impact of food limitation on development of the Arctic endemics so that the temperature-dependent simulations present a best-case scenario. Nonetheless, these distributions fit well with the observed distributions of *C. glacialis* that is known to be most abundant along the margins of the central Arctic, in the slope and shelf regions, with reduced abundances in the central Arctic (e.g., Smith and Schnack Schiel, 1990; Ashjian et al., 2003; Hirche and Kosobokova, 2007; Kosobokova and Hirche, 2009). It was startling that *C. hyperboreus* could not achieve the first diapause stage (from N3 to C3) in the Central Arctic in the first simulations (temperature-dependent development only at the surface and at 50 m), since this species is believed to be prevalent in the central Arctic (e.g., Falk-Petersen et al., 2009; Kosobokova and Hirche, 2009). This suggested that the ability of the Arctic endemic to succeed in the short growth season of the central Arctic is tenuous at best. Dawson (1978) observed that one year's brood of *C. hyperboreus* from the location of the ice island T-3 apparently failed, implying that for some years recruitment is not successful. Moreover, it has been proposed that both *C. hyperboreus*, and *C. glacialis* are not endemic to the central Arctic but rather are advected into the region in surface currents (Ollie et al., 2007). Advection at depth during overwintering (Fig. 8) clearly expanded the distribution of these species northward, especially in strong currents, but the locations reached were those where successful recruitment to the diapausing stage was not possible (Fig. 7). An explanation for the discrepancy between observed and modeled results may lie in the fact that *C. hyperboreus* has a multi-year life cycle. The critical stage for diapause appears to be C3 in the first year. For the next two to three years it can then overwinter in stages C4, C5 or C6, while being transported throughout the central Arctic. Whether or not the next generation is able to successfully recruit would then depend on where in the central Arctic the eggs are produced. This would likely produce a distribution of *C. hyperboreus* throughout the central Arctic, but with successful recruitment only in limited areas. For *C. glacialis*, a similar but more limited distribution pattern may occur given a shorter 2-year life cycle and longer critical development times.

The more limited distribution of successful diapause in regions with short growth seasons in the central Arctic for *C. glacialis* relative to *C. hyperboreus* (Fig. 7) can be explained by shorter critical development times, even on the order of days, for *C. hyperboreus* (Fig. 2f). Although total development time is longer for *C. hyperboreus* (Fig. 2e), the life history traits of lipid based egg production and early copepodid (C3) diapause result in a shorter first year critical development time. If the Arctic endemic *C. glacialis* consistently utilizes lipid-reserves for egg production as has been suggested for early season egg production (Smith, 1990; Hirche and Kattner, 1993; Kosobokova, 1999; Niehoff et al., 2002; Hirche and Kosobokova, 2003), thus shortening the critical development time since food would only be required at N3, then the critical development is reduced and this species would require a shorter growth season and the distribution of locations at which diapause can be achieved is expanded northwards into the central Arctic, similar to that of its Arctic congener. Lipid-based reproduction then may be a strategy that enables *C. glacialis* to persist at the boundaries of the central Arctic. Although lipid-based reproduction prior to the spring bloom has been deduced from stage development in several regions (e.g., Hirche and Kattner, 1993; Kosobokova, 1999; Niehoff et al., 2002; Hirche and Kosobokova, 2003), few measurements of egg production pre-bloom exist (e.g., Smith, 1990) and the frequency and importance of this early season reproduction to the overall reproductive output of *C. glacialis* populations remains poorly understood. However, since *C. glacialis* is much less abundant than *C. hyperboreus* in the central Arctic, it seems likely that lipid-based reproduction does not represent significant recruitment for *C. glacialis.*

Both *C. glacialis* and particularly *C. hyperboreus* responded to an increase in the length of the growth season (Fig. 9) and to warmer water temperature (Fig. 10) with northward expansion of the regions of successful diapause, indicating that the present growth season and water temperature are very close to conditions that permit colonization of almost the entire central Arctic. It is possible that these species undergo unreliable recruitment in the central Arctic, with populations there augmented and maintained by advection of allochthonous individuals but with localized regions of autochthonous and episodic recruitment as well.

Atlantic endemic – Calanus finmarchicus

Calanus finmarchicus is believed to be an expatriate species in the Arctic Ocean and marginal seas, with the population being advected into the Barents Sea from the Norwegian Sea and into the Eurasian Basin through Fram Strait (Jaschnov, 1970; Conover, 1988; Hirche and Kosobokova, 2007). It is not found throughout the Arctic Ocean, although it can be transported considerable distances along the margins in circulation of Atlantic Water (e.g., Kosobokova and Hirche, 2009). These known distributions correspond fairly well to locations where *C. finmarchicus* can successfully achieve diapause in the simulations.

Compared to its Arctic Ocean endemic congeners *C. glacialis* and *C. hyperboreus, C. finmarchicus* is smaller, slower growing at low temperatures, and better adapted to warm water conditions (Fig. 2). Low temperatures had been suggested as the major cause for low growth, and possibly reproductive failure, and therefore the inability of *C. finmarchicus* to sustain itself in the Arctic Ocean and marginal seas (Jaschnov, 1970, Sameoto, 1984; Tande et al., 1985; Hansen et al., 1996). However, female *C. finmarchicus* can continue to spawn at very low temperatures (-1 to +1 °C) with egg production rates at -1.5 to 2 °C similar to those of *C. glacialis* (Hirche, 1990; Hirche et al., 1997). Late availability of food rather than low temperature alone was hypothesized to limit reproductive success and hence the sustainability of the *C. finmarchicus* in the Arctic Ocean (Hirche and Kosobokova, 2007). This is consistent with the results of the present study that indicate that the duration of the growth season, defined as the period during which chlorophyll (and likely microzooplankton) food is available, is a critical factor in determining successful recruitment.

Even without considering the low temperature- and/or food- induced reproduction failure, the simulations show that slow development rate at low temperature alone can limit the expansion of *C. finmarchicus* to the north (Fig. 5). If the additional food-dependent development is invoked in the simulations, the population is much more constrained in the southern part of the GIN Seas, Barents and Kara Seas (Fig. 6). Most of the individuals found along the Eurasian margins of the central Arctic are in C5 and adult stages (Kosobokova et al., 1998; Hirche and Kosobokova 2007; Kosobokova and Hirche; 2009). The absence of young copepodids suggests that the population in those areas are either not reproducing or cannot even reach copepodite stages after hatching. The C5 and adult individuals observed by Kosobokova and Hirche (2009) along the northern edge of Barents, Kara Sea, and Laptev seas, are probably the result of continuous advection from more southern regions of those individuals that emerge from diapause after winter. The overwintering simulation (Fig. 8) demonstrated northward range expansion for *C. finmarchicus* consistent with these observations. Note, however, that all of these newly reached locations were identified as inhospitable for successful recruitment in the simulations because the growth seasons there were too short to permit successful development to the diapause stage at the ambient temperatures and food concentrations.

Our results suggest that *C. finmarchicus* is unable to penetrate, survive, and colonize the Arctic Ocean under present conditions of temperature, food availability, and length of the growth season because of a combination of factors. The copepods cannot reach the diapausing stage under the conditions experienced in the northern portions of the GIN and Barents Seas. In addition, the prevailing circulation is not fast enough to advect the copepods into the Arctic Ocean during the growth season, or even during the winter following, at the depths the copepods are believed to diapause (Fig. 8). This scenario is not likely to change even if the water temperature increases by 2°C across the region.

Pacific endemic - Calanus marshallae

It has been hypothesized that ongoing climate change could result in the immigration and establishment of expatriate species such as *C. marshallae* into the Arctic Ocean from surrounding sub-arctic regions. The Western Arctic region is particularly susceptible to such community composition shifts because of the persistent inflow of Pacific Water from the northern Bering Sea through the Bering Strait and northward through the Chukchi Sea. Pacific Ocean copepod species, including those of genera other than *Calanus*, have been observed in the Chukchi and Beaufort Seas previously (e.g., Ashjian et al., 2003; Cooper et al., 2006; Lane et al., 2007; Hopcroft and Kosobokova, 2009; Nelson et al., 2009; Hopcroft et al., 2010). The Pacific species *C. marshallae* was reported from a sample collected in Svalbard based on genetics (Sundt & Melle, 1998), leading to speculation that advection of this species into and across the Arctic Ocean had occurred and that successful colonization of the Arctic Ocean by this species was possible under ocean warming. However, colonization can only be accomplished if a species can successfully reproduce. The present study demonstrated that few *C. marshallae* in the central Arctic successfully reached diapause (note difference between distributions of starting locations (Fig. 3a) and of those where *C. marshallae* can reach diapause (Figs. 5a, 6), even under warming or with an extended growth season length

(Figs. 9a, 10a)). Those that did reach diapause in the central Arctic have been advected to locations at which individuals that start there cannot successfully develop to diapause, so these individuals would be present but could not persist at those locations. Furthermore, advection across the central Arctic cannot be accomplished without a period of overwintering because of the long transit times (years) involved. Ecologically then it is highly unlikely that the individuals observed at Svalbard could have been advected across the Arctic Ocean from the Pacific.

Potential Impacts of Climate Change

Lengthening of the growth season and ocean warming in the simulations not only demonstrated the sensitivity of the Arctic endemics to subtle variations in the environment, but also predicted some potential impacts that might result in response to climate change. Small changes in seasonality that could lengthen the growth season and increases in water temperature could result in successful recruitment of these large bodied grazers, particularly *C. hyperboreus*, more consistently over a large portion of the Central Arctic. Whether sufficient primary production will occur in that region to support an increased biomass of these copepods is unknown. With ocean and atmosphere warming through climate change come also modification in the timing and extent of seasonal sea ice cover that could have significant changes on the timing of spring ice-edge and open-water phytoplankton blooms (e.g., Arrigo et al., 2008, Kahru et al., 2011). These in turn could lead to a mis-match between plankton life histories and the availability of food. The timing of the spring bloom, and of copepod egg production, could be the critical factor in determining whether *Calanus spp.* can recruit and persist in arctic or sub-arctic seas (e.g., Melle and Skjoldal, 1998; Hirche and Kosobokova, 2007; Varpe et al., 2007; Falk-Petersen et al., 2009; Varpe et al., 2009; Søreide et al., 2010), with changes in spring bloom timing as a result of changes in sea ice potentially leading to recruitment failure. Alternatively, both *C. glacialis* and *C. finmarchicus* have been shown to recruit earlier in response to earlier availability of food in the North Water Polynya (Ringuette et al., 2002), suggesting a plasticity in their life histories that may permit adaptation to changing seasonality under climate change.

Limitations of the modeling approach

Coupling individual based development rates to modeled circulation was an effective means to explore the underlying life history parameters and environmental dependencies of the different copepod species that result in the observed biogeographic distributions of each species at present and the potential change in those distributions under climate change. However, limitations to the modeling must be considered when evaluating the results of the simulations. First, food dependent development rates are difficult to estimate because 1) the satellite-derived chlorophyll could be highly biased at high latitudes (Gregg and Casey, 2007); and 2) chlorophyll food concentrations in the ice-covered central Arctic are not available. This could be overcome through increased availability of chlorophyll data from those regions, and incorporation of such data into an annual basin-wide chlorophyll climatology, however this is not likely to be achieved in the near future. Additionally, coupling individual based development rates to the output of biological-physical ecosystem models, rather than to a physical ice-ocean model only, could provide modeled chlorophyll concentrations to the daily development increments.

If food-dependent, in addition to temperature-dependent, development was included for the Arctic endemics, the range of distributions of where the Arctic endemics could achieve diapause would likely be constrained since the present simulations assume that food is not limiting. Second, the development rate coefficients for all of the species were dependent on extrapolations from limited observational data on egg production and the equiproportional rule. As a result, there could be errors in the stage-specific development rates and that would alter the results of the simulations. In particular, unique development rate coefficients could not be identified for *C. marshallae* because appropriate experimental data were not available for this species. Egg production and development experiments at the full range of the environmental temperatures with all species, and especially with *C. marshallae,* are necessary to provide the needed data to develop these coefficients. Additionally, the diapause stage is simply set to a certain copepodid stage in the model without considering the behavior and physiological conditions (e.g. lipid). This simplification can cause additional uncertainty in the simulation. Third, for each species we chose to use the predominate stage of first diapause from field observations to determine the critical development time, assuming that younger stages would be less fit for surviving the over-wintering period. If under certain conditions these younger stages can survive, the critical development time would be reduced allowing for survival in regions with a shorter growth season. Fourth, the warming scenario did not include changes in ice coverage and food availability that might occur concurrent with an increase in water temperature and attendant change in seasonality. Again, this might be overcome by using an ecosystem model coupled with the individual based development modeling, if such modeling efforts are believed to provide realistic predictions regarding these biological and physical changes. Fifth, uncertainty exists regarding the start date of the growth season both in ice-free and ice-covered regions. Water column chlorophyll, here measured from satellite ocean color, may not be completely accurate and does not reflect potential availability of other prey types (e.g., microzooplankton) or availability of chlorophyll at depth or associated with sea ice (ice algae). The use of the timing of snowmelt to determine growth season start date in ice-covered regions likewise suffers from potential limitations. Food may be available for copepod growth prior to complete snowmelt, such as primary production by ice algae under the ice and potentially by phytoplankton in sea ice leads that would extend the length of the growth season. The expansion in the range where diapause of the Arctic endemics could be initiated when the growth season is lengthened by just two weeks demonstrates the sensitivity of the life histories to the timing of food and the importance of determining the length of the growth season as accurately as possible. Sixth, development in the Arctic endemic *C. glacialis* was assumed to start with the onset of food dependent egg production, however this species may utilize lipid-reserves for egg production (e.g., Smith, 1990; Hirche and Kattner, 1993; Kosobokova, 1999; Niehoff et al., 2002; Hirche and Kosobokova, 2003; Falk-Peterson et al., 2009); such a strategy would result in development of individuals starting earlier at some locations than the start of the growth season. This could extend the potential period over which advection and expansion of range could occur by several weeks since food would not be required by the lipid-produced eggs until the first naupliar feeding stage (N3), which would be achieved as much as six-seven weeks after egg production, depending on water temperature (Fig. 2b). Finally, the simulations represent in many aspects the "best-case" scenario, with reproduction initiated immediately upon the availability of food and with food-dependence not included for the Arctic endemics. Also, no area- and stage- dependent mortality is included in the model, so its constraints to the boundary expansion of the different species are not considered and should be tested in future studies.

5. Conclusion

The modeling study demonstrated that the present geographic distributions of the four species in the Arctic, and particularly in the central Arctic, are consistent with the patterns derived from a model based simply on development rates, life histories, and the length of the growth season at each location. The critical development time of the Arctic endemics appeared to be closely aligned with the length of the growth season, so closely that a change in growth season length on the order of days would significantly impact the species' ability to recruit and persist at that location. This suggested also that the sustainability of populations of Arctic endemics in the central Arctic is uncertain, with interannual variability in recruitment success likely. Furthermore, changes in the growth season length in response to changing seasonality could have significant impacts on the distributions and persistence of these species in the central Arctic. The critical development time of the two expatriate species were less well suited to the length of the growth season in the Arctic, being much longer than the growth season at most locations in the central Arctic and at many locations in the marginal seas. Only in regions with localized enhancement of the growth season length, such as polynyas or in currents with elevated food, were the expatriates able to successfully reach diapause. Thus subtle changes in the length of the growth season or in water temperature with associated decreases in development time likely would not result in a significant change in the expatriate species distributions.

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Table 1. Development-temperature function parameters (‘a’ value in Equation 2)

Species	**Egg**	**N1**	**N2**	**N3**	**N4**	**N5**	**N6**	**C1**	**C2**	**C3**	**C4**	**C5**
Calanus finmarchicus	595	388	581	1387	759	716	841	966	1137	1428	2166	4083
Calanus Glacialis	839	548	819	1958	1070	1011	1186	1363	1605	2014	3057	5761
Calanus Hyperboreus	1495	974	1461	3485	1907	1799	2113	2427	2856	3588	5443	10259

Table 2. Simulations conducted and critical start/end life stages for the four *Calanus* species. Depths at which copepods were maintained for each simulation are shown. Unless otherwise noted, growth season and starting locations were defined using SeaWiFS derived chlorophyll *a* for *C. finmarchicus* and *C. marshallae* and using snowmelt and radiation for *C. glacialis* and *C. hyperboreus*. ‘*’ Denotes conditions/species for which simulations were run using both methods to define the growth season and starting locations.

Species	**Development**		**Diapause**	**A) Earlier Growth Season Start**	**B) Warming**	**Both A) and B)**	**Start Stage**	**Diapause Stage**
	Temperature-Dependent	Temperature- and Food-Dependent						
C. finmarchicus	0 m* 50 m	0 m 50 m	200 m	0 m	0 m	0 m	Egg	C5
C. marshallae	0 m* 50 m	0 m 50 m	200 m	0 m	0 m	0 m	Egg	C5
C. glacialis	0 m 50 m	- -	200 m	0 m	0 m	-	Egg	C4, C5
C. glacialis	0 m	-	-	-	-	-	N3	-
C. hyperboreus	0 m 50 m	- -	200 m	0 m	0 m	-	N3	C3, C4

Figure Captions

Figure 1. Pan-Arctic region showing the model triangle mesh node points (black dots). GIN Sea represents Greenland-Iceland-Norwegian Sea.

Figure 2. Belehrádek's curves for three species of *Calanus*. Upper row shows dependence on temperature of development rate for each life stage of each species. Lower row shows development time from egg to naupliar stage 6 over a range of temperatures (left), over all life stages (egg-adult; middle) and critical development time (right, see text for definition). The first diapausing stage was specified as C5 for *C. finmarchicus*, C4 for *C. glacialis*, and C3 for *C. hyperboreus*.

Figure 3. Growth season start dates and lengths for locations in seasonally (a, c) and perennially (b, d) ice covered regions. Initial release date (year day): (a) based on the SeaWiFS-derived chlorophyll *a* concentration; (b) based on the onset of snowmelt. Growth season length (days): (c) based on the SeaWiFS-derived chlorophyll *a* concentration; (d) based on snow melt and shortwave radiation.

Figure 4. Climatological monthly mean sea surface temperature and residual flow in April and September. White vectors: velocity >= 5 cm s^{-1}; black vectors: velocity < 5 cm s^{-1}.

Figure 5. Locations where *C. finmarchicus* (Atlantic side) and *C. marshallae* (Pacific side) successfully reached diapause while being advected at surface: (a) using onset of snow melt and (b) using SeaWiFS chlorophyll *a* as the growth season proxy and for starting locations. Development was temperature dependent only. Blue dots: release locations; Red dots: end locations at the end of growth season.

Figure 6. Locations where *C. finmarchicus* (Atlantic side) and C. *marshallae* (Pacific side) successfully reached diapause under temperature and food dependent development (a) at the surface and (b) at 50 m below the surface using SeaWiFS chlorophyll *a* as the growth season proxy and food supply and to define starting locations. Blue dots: release locations; Red dots: end locations at the end of growth season.

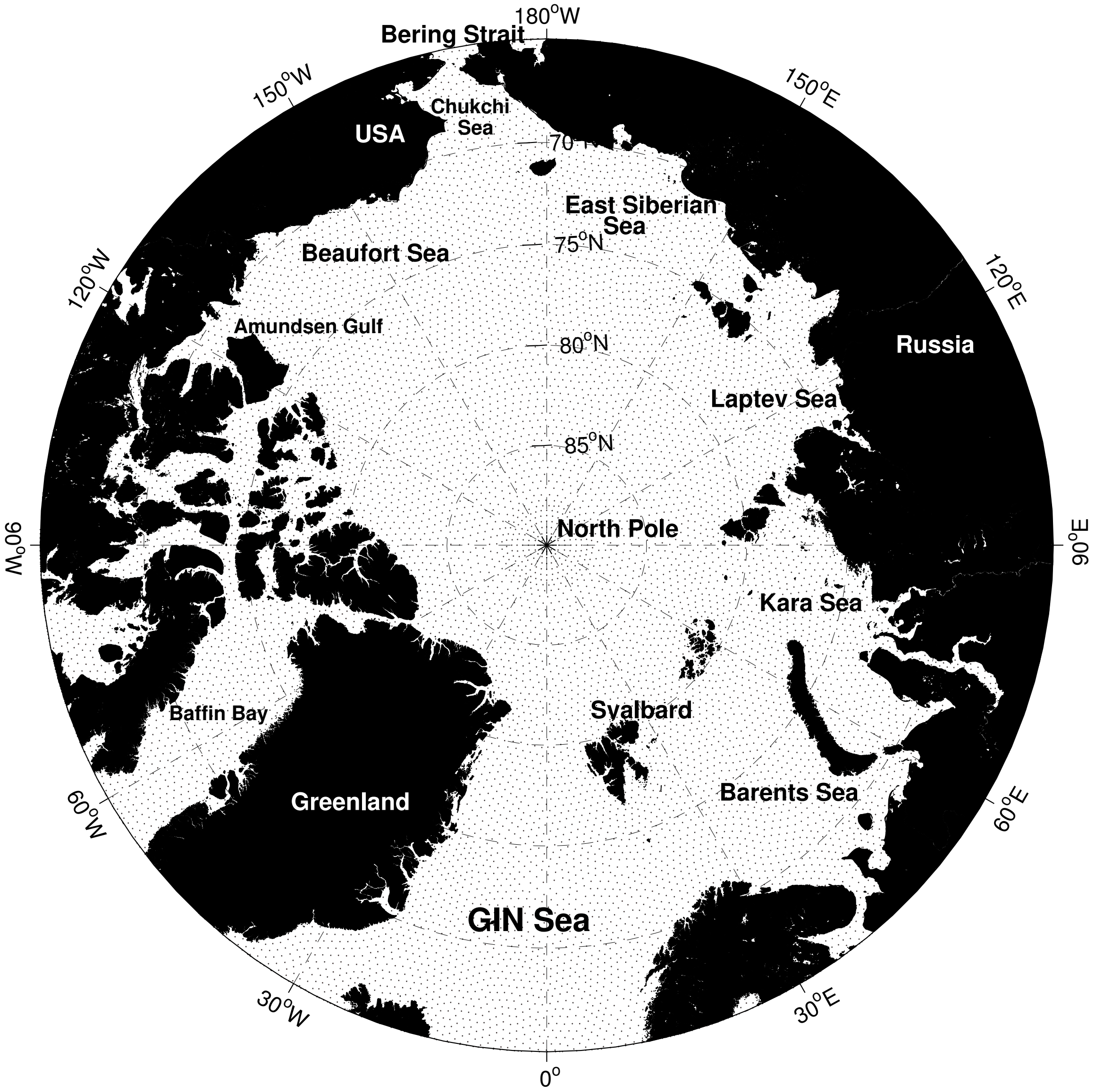
Figure 7. Locations where (a) *C. glacialis* and (b) *C. hyperboreus* successfully reached diapause at the surface under temperature dependent development only using snow melt/irradiance as the growth season proxy and to define starting locations. Blue dots: release locations; Red dots: end locations at the end of growth season.

Figure 8. Locations reached by (a) *C. finmarchicus* (Atlantic side) and *C. marshallae* (Pacific side) after the first year diapause, using the chlorophyll *a* criterion for the growth season and (b) *C. glacialis* after the second year diapause and (c) *C. hyperboreus* after the third year diapause; both using the snow melt/irradiance criterion for the growth season. All diapausing individuals stay at 200 m (for waters deeper than 200 m) or 5 m above the bottom (for waters shallower than 200 m). Blue dots: release locations determined from

the end location of individuals reached diapause stage at the end of the growth season; red dots: end locations.

Figure 9. Locations where individuals reached diapause at the surface with the growth season starting two weeks earlier than the date identified by the chlorophyll *a* criterion for (a) *C. finmarchicus* (Atlantic side) and *C. marshallae* (Pacific side) and for the snow melt/irradiance criterion (b) *C. glacialis* and (c) *C. hyperboreus*. Blue dots: release locations; red dots: end locations.

Figure 10. Locations where individuals reached diapause at the surface under temperatures 2 °C warmer than the climatology for (a) C. *finmarchicus* (Atlantic side) and *C. marshallae*, (b) *C. glacialis*, (c) *C. hyperboreus* and (d) same as (a), but starts the growth season two weeks earlier. Blue dots: release locations; Red dots: end locations at the end of growth season.



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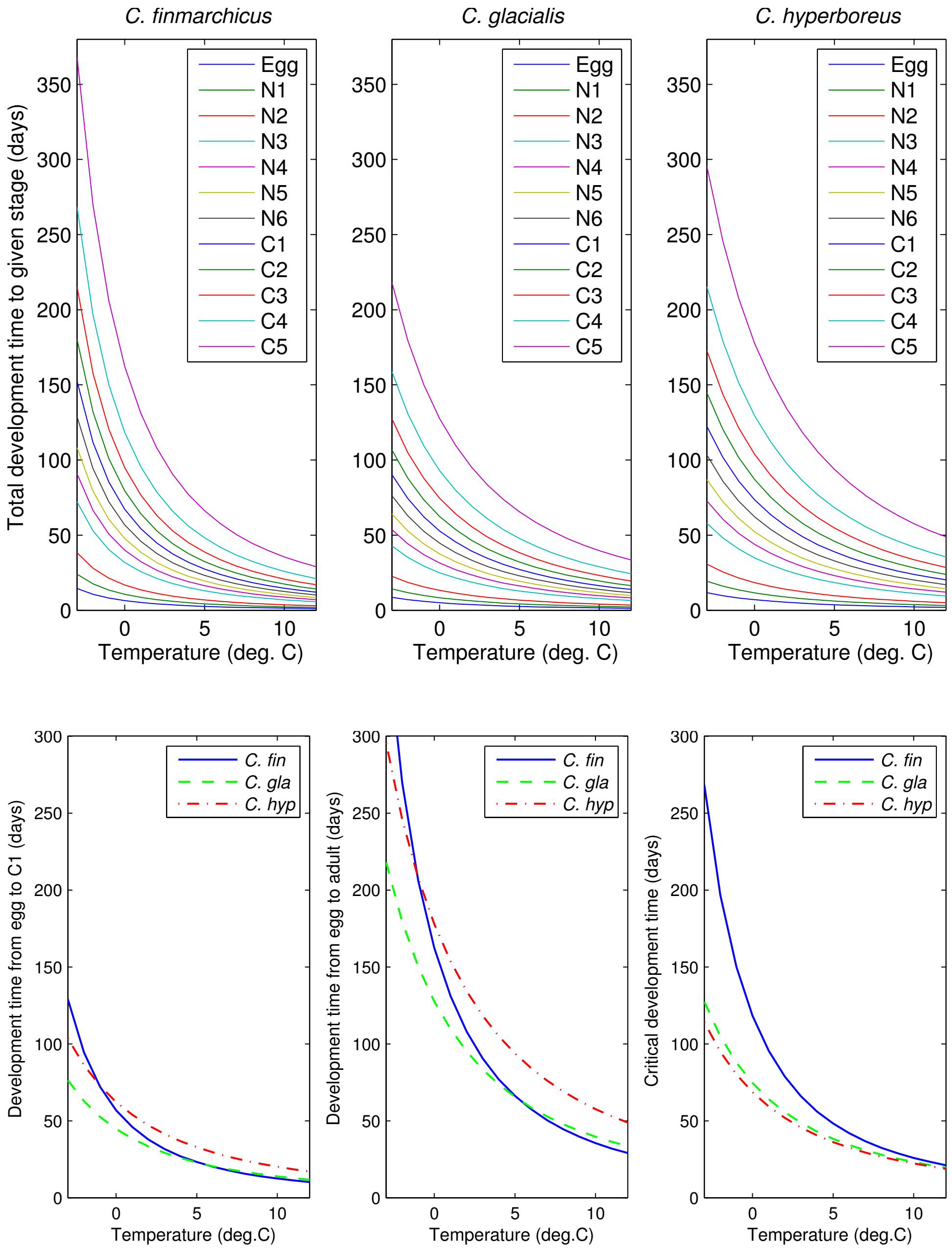

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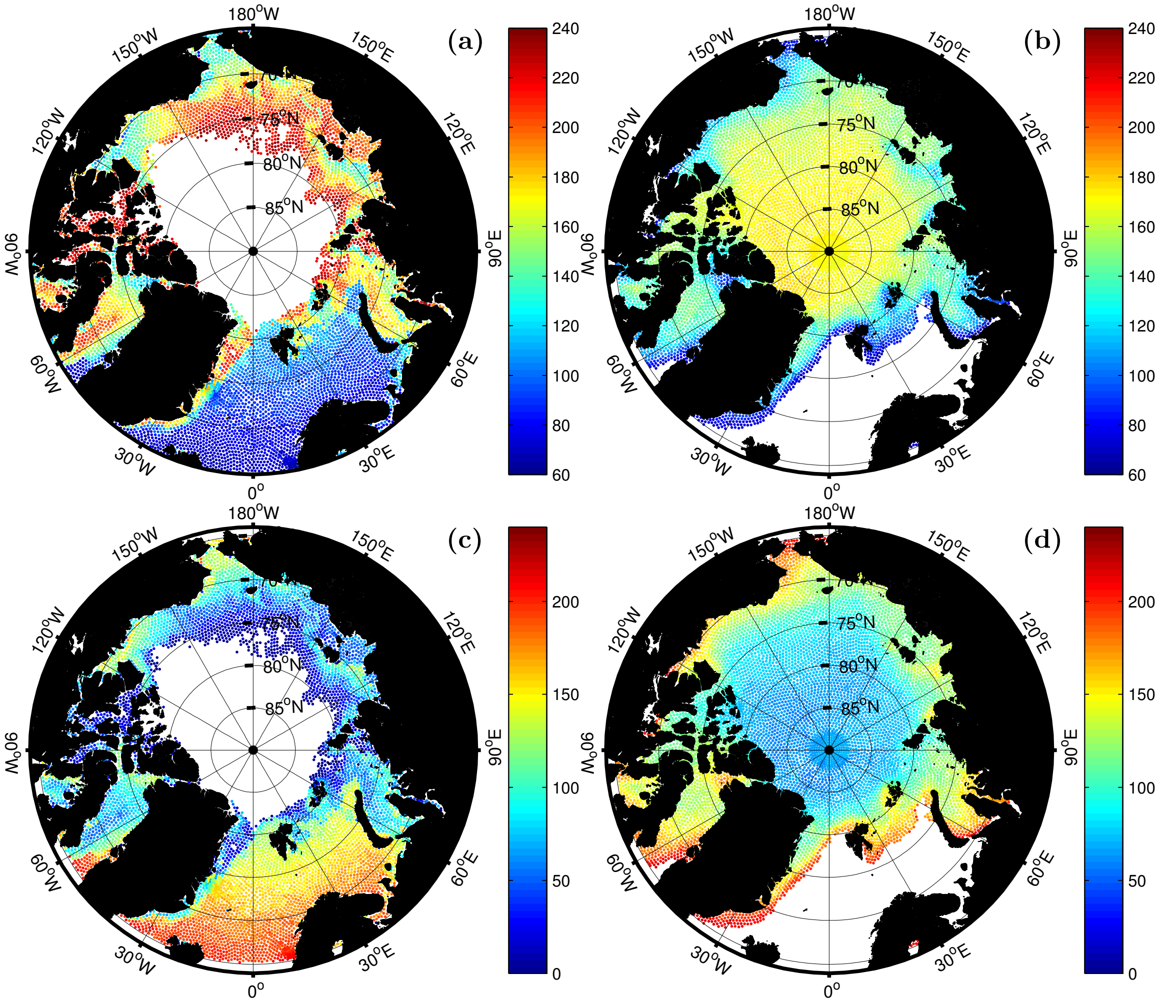

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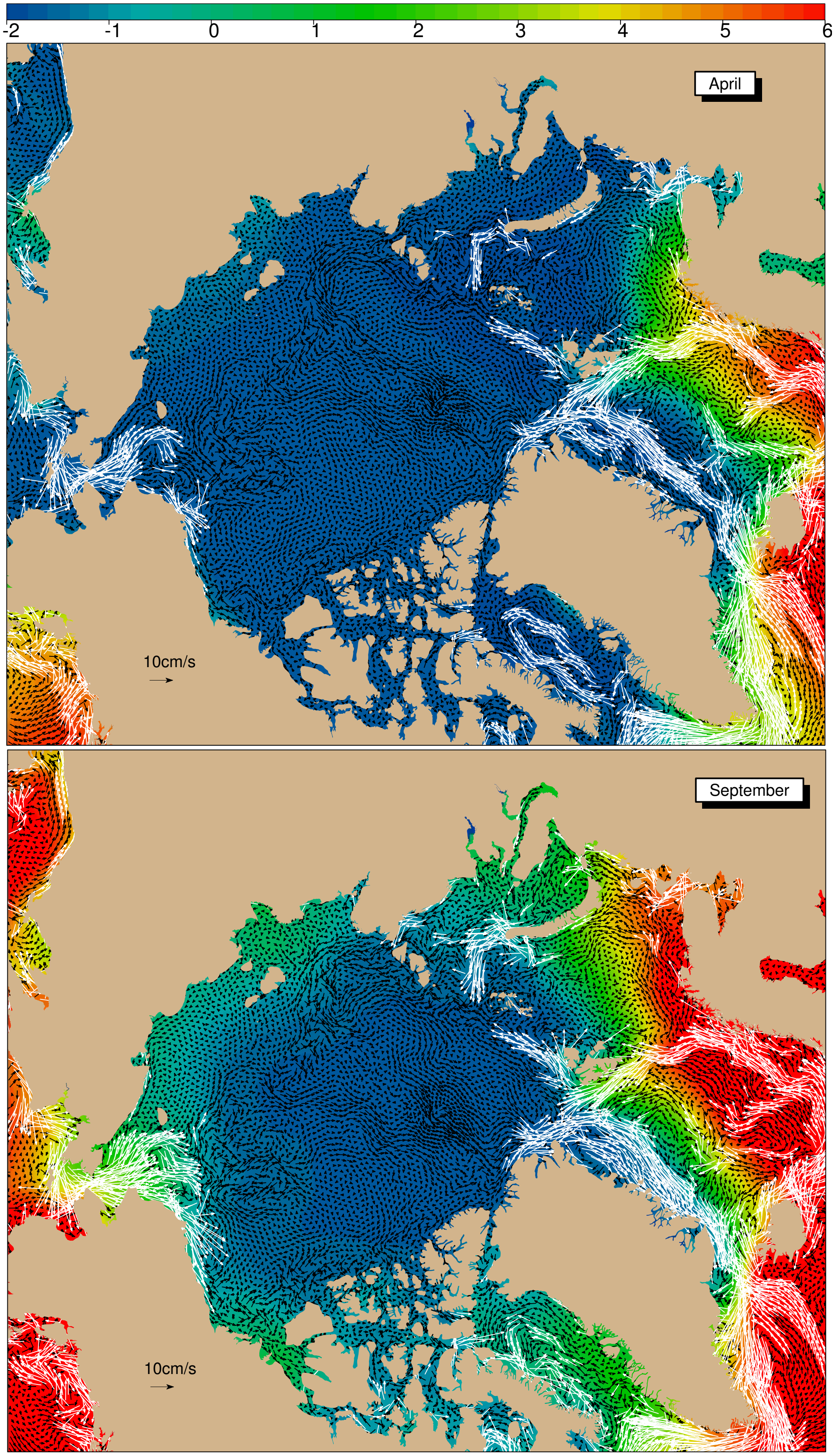

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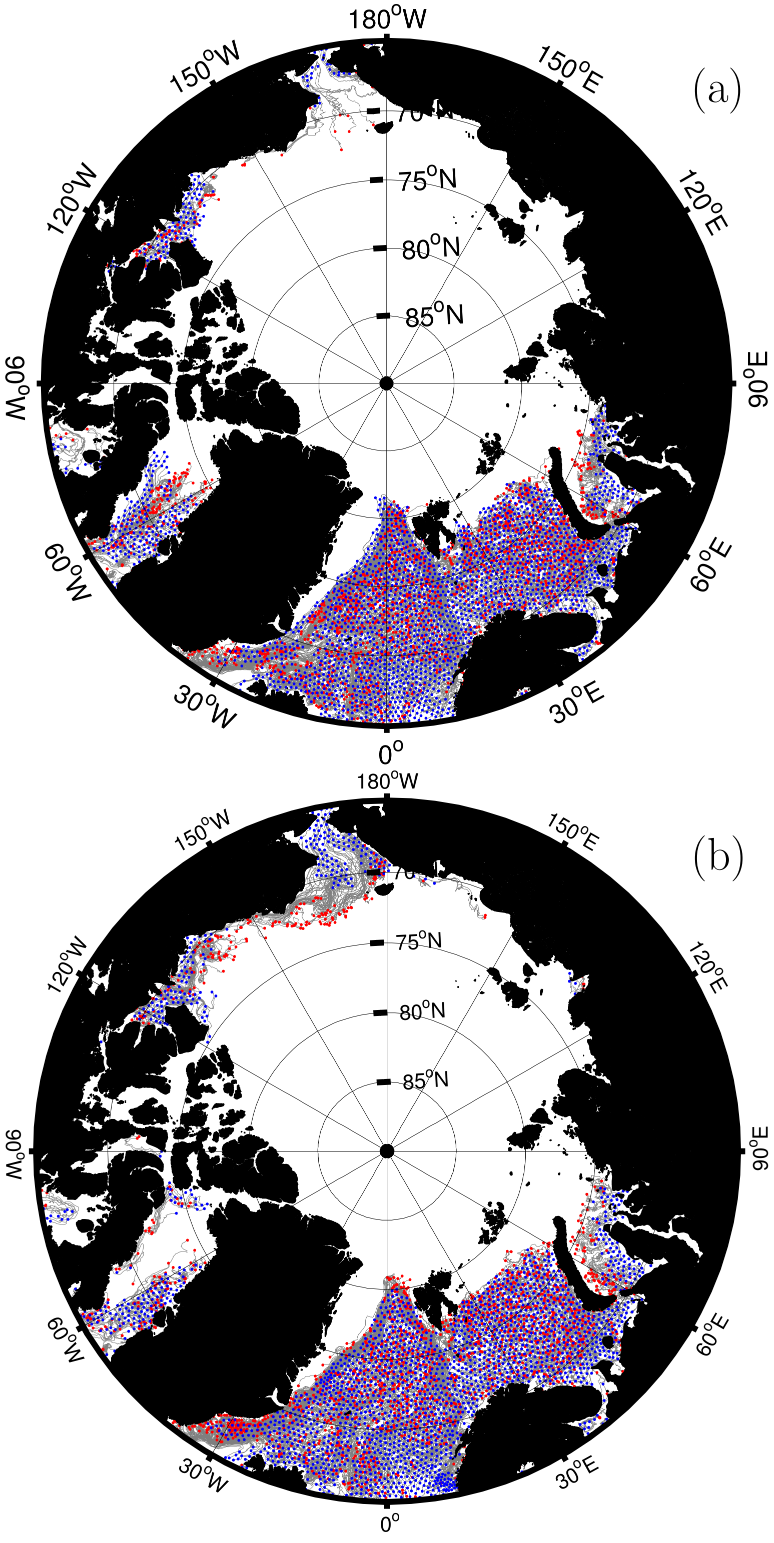
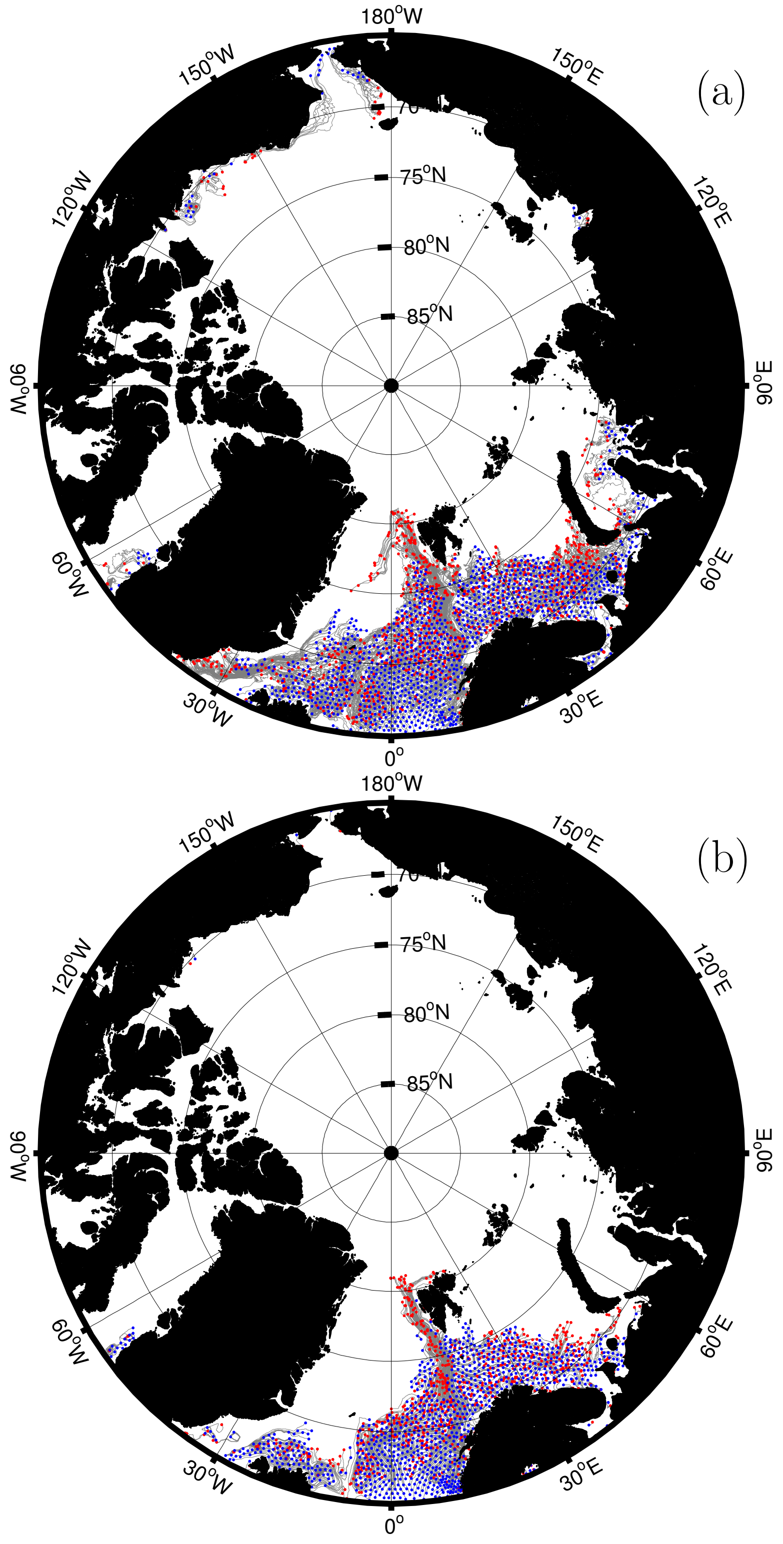


Figure 5: Locations where *C. finmarchicus* (Atlantic side) and *C. marshallae* (Pacific side) successfully reached diapause while being advected at surface: (a) using both the onset of snow melt and SeaWiFS chlorophyll *a* as growth season proxy and (b) using SeaWiFS chlorophyll *a* as the growth season proxy and for starting locations. Development was temperature dependent only. Blue dots: release locations; Red dots: end locations at the end of growth season.



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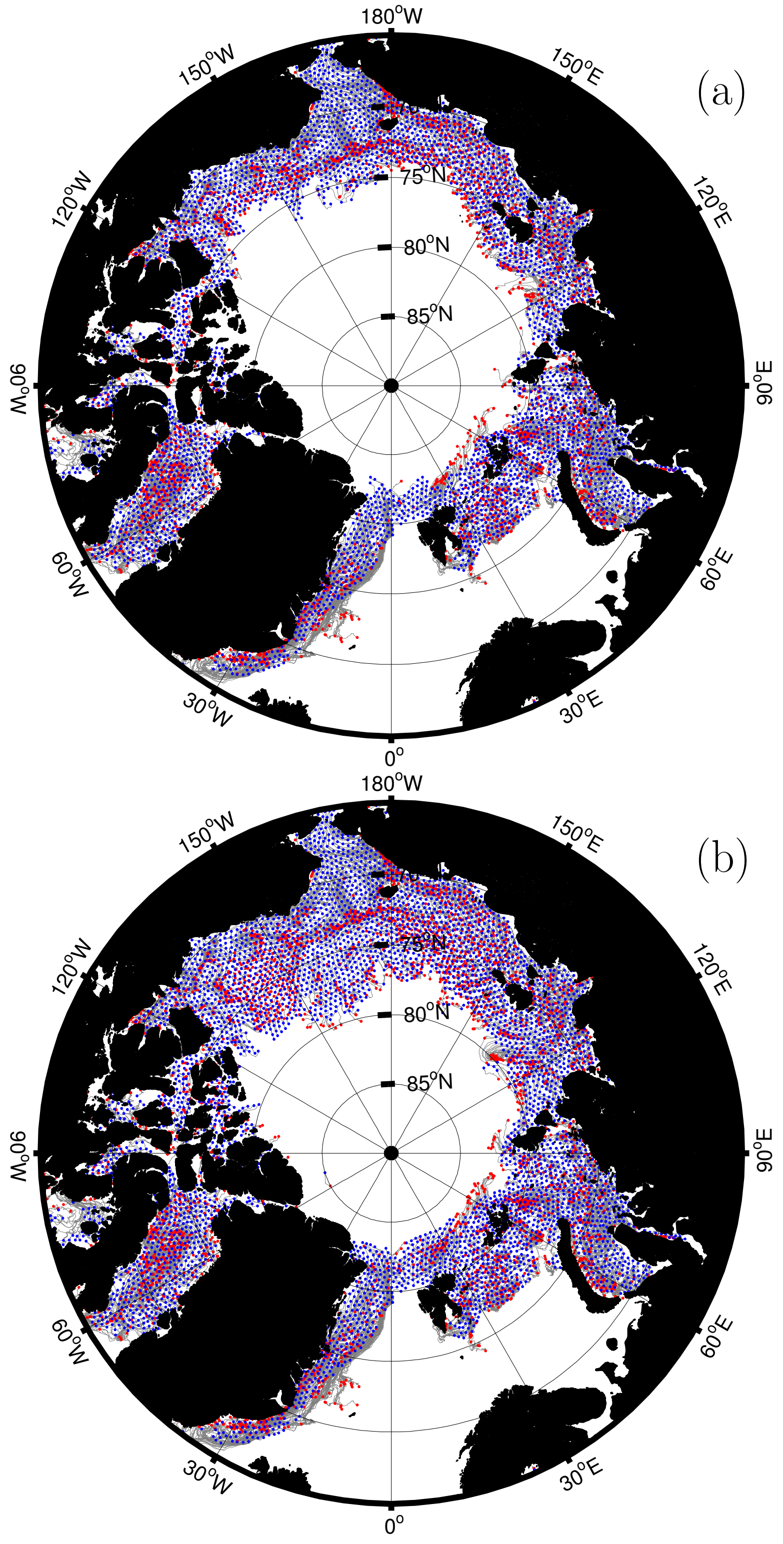

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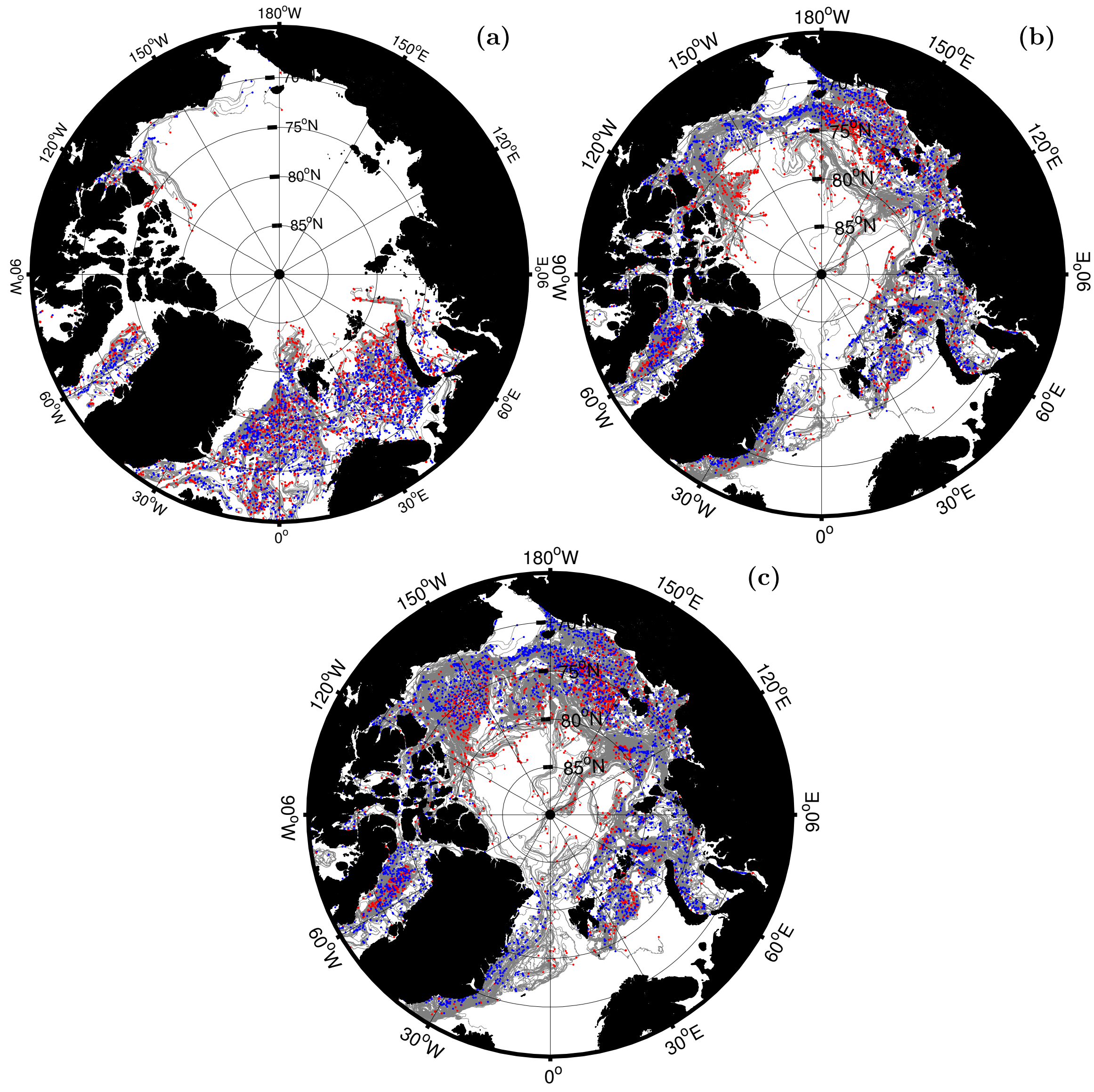

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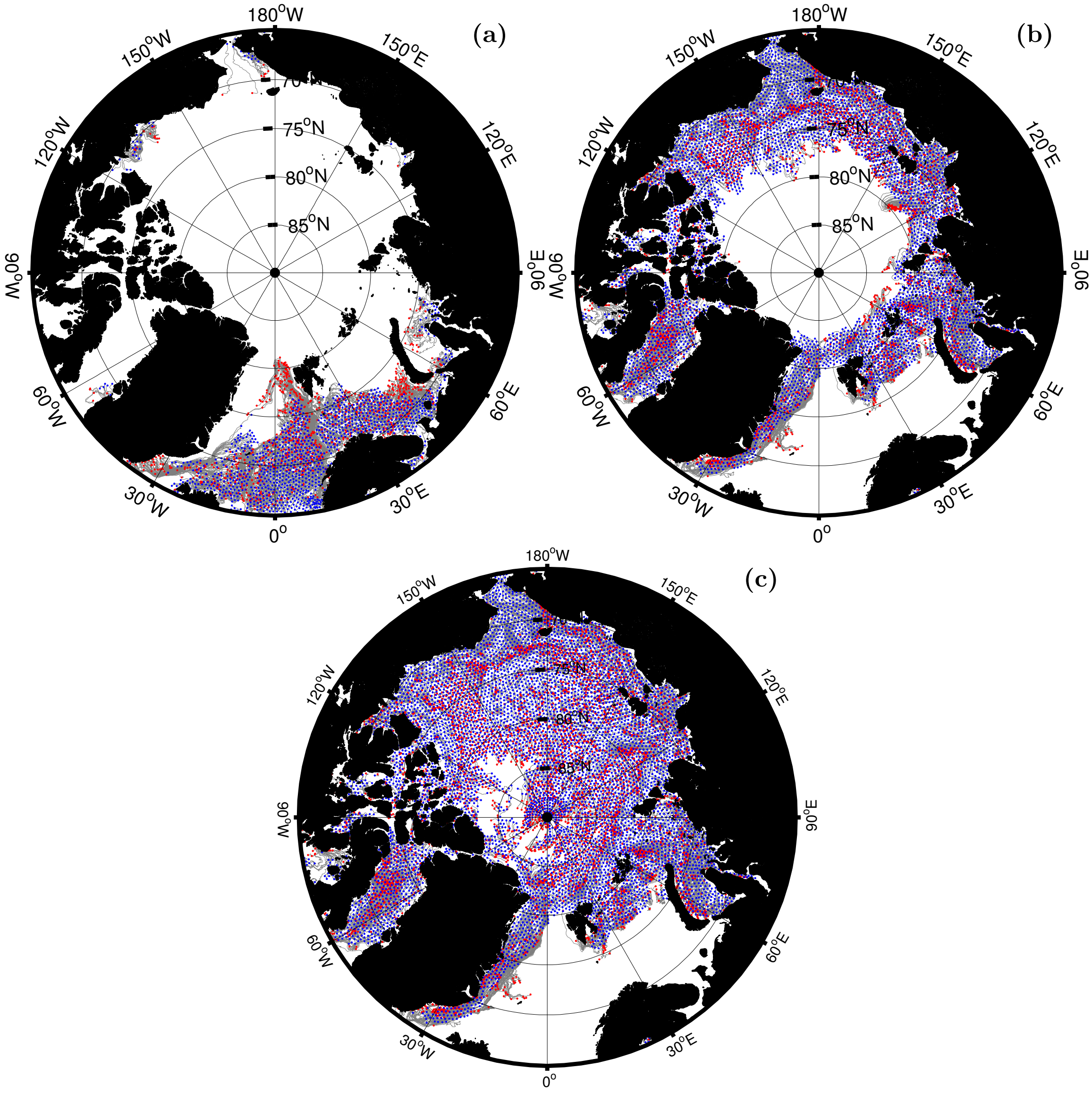

Figure 9: Locations where individuals reached diapause at the surface with the growth season starting two weeks earlier than the date identified by the chlorophyll *a* criterion for (a) *C. finmarchicus* (Atlantic side) and *C. marshallae* (Pacific side), and for the snow melt/irradiance criterion (b) *C. glacialis* and (c) *C. hyperboreous*. Blue dots: release locations; Red dots: end locations at the end of growth season.

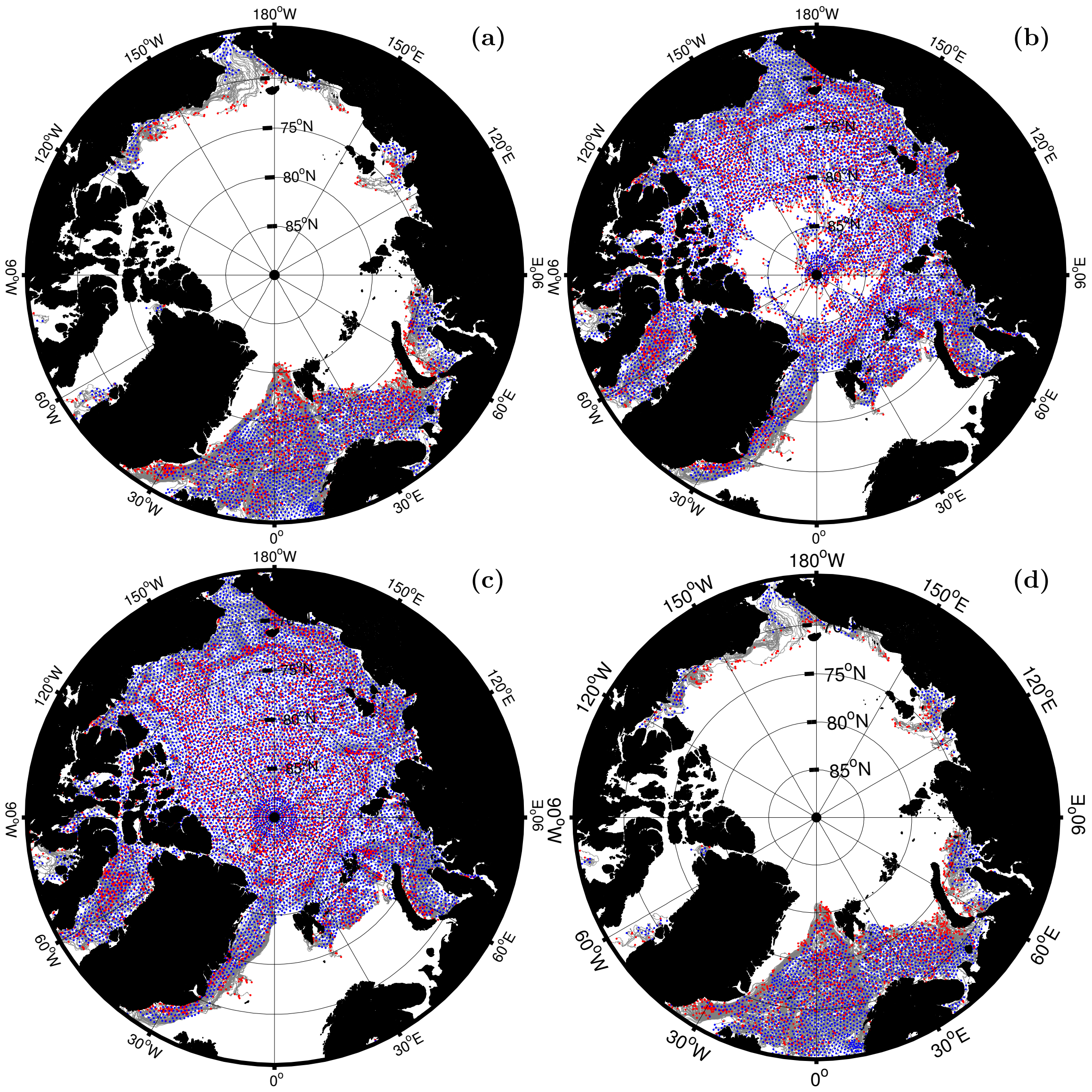

Figure 10: Locations where individuals reached diapause at the surface under temperatures 2 ^{o}C warmer than the climatology for (a) *C. finmarchicus* (Atlantic side) and *C. marshallae* (Pacific side), (b) *C. glacialis*, (c) *C. hyperboreous* and (d) same as (a), but starts the growth season two weeks earlier. Blue dots: release locations; Red dots: end locations at the end of growth season.