

RESEARCH ARTICLE

10.1002/2016JC011784

Key Points:

- Life history development of Arctic endemic copepod *C. glacialis* is modeled
- Ocean warming and early ice retreat may expand *C. glacialis* distribution poleward
- Northernmost *C. glacialis* individuals are most susceptible to environmental variability

Supporting Information:

- Supporting Information S1

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Citation:

Feng, Z., R. Ji, R. G. Campbell, C. J. Ashjian, and J. Zhang (2016), Early ice retreat and ocean warming may induce copepod biogeographic boundary shifts in the Arctic Ocean, *J. Geophys. Res. Oceans*, 121, doi:10.1002/2016JC011784.

Received 11 MAR 2016

Accepted 20 JUL 2016

Accepted article online 25 JUL 2016

Early ice retreat and ocean warming may induce copepod biogeographic boundary shifts in the Arctic Ocean

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Abstract Early ice retreat and ocean warming are changing various facets of the Arctic marine ecosystem, including the biogeographic distribution of marine organisms. Here an endemic copepod species, *Calanus glacialis*, was used as a model organism, to understand how and why Arctic marine environmental changes may induce biogeographic boundary shifts. A copepod individual-based model was coupled to an ice-ocean-ecosystem model to simulate temperature- and food-dependent copepod life history development. Numerical experiments were conducted for two contrasting years: a relatively cold and normal sea ice year (2001) and a well-known warm year with early ice retreat (2007). Model results agreed with commonly known biogeographic distributions of *C. glacialis*, which is a shelf/slope species and cannot colonize the vast majority of the central Arctic basins. Individuals along the northern boundaries of this species' distribution were most susceptible to reproduction timing and early food availability (released sea ice algae). In the Beaufort, Chukchi, East Siberian, and Laptev Seas where severe ocean warming and loss of sea ice occurred in summer 2007, relatively early ice retreat, elevated ocean temperature (about 1–2°C higher than 2001), increased phytoplankton food, and prolonged growth season created favorable conditions for *C. glacialis* development and caused a remarkable poleward expansion of its distribution. From a pan-Arctic perspective, despite the great heterogeneity in the temperature and food regimes, common biogeographic zones were identified from model simulations, thus allowing a better characterization of habitats and prediction of potential future biogeographic boundary shifts.

1. Introduction

The Arctic Ocean has been undergoing rapid and dramatic changes in the past few decades. The most evident change is the loss of sea ice [Stroeve *et al.*, 2012]. Since the start of satellite monitoring in the late 1970s, March and September ice extents have been declining at average rates of 2.8 and 11.3% per decade, respectively [Perovich and Richter-Menge, 2009], with record low summer sea ice extents in Septembers 2007 and 2012 [Comiso *et al.*, 2008; Zhang *et al.*, 2013]. This reduction of ice cover is associated with increased ocean primary production over large areas of the Arctic shelf seas as shown by both ocean color satellite observations [Arrigo *et al.*, 2008; Pabi *et al.*, 2008; Arrigo and van Dijken, 2011; Brown and Arrigo, 2012] and fully coupled biophysical ecosystem models [Wassmann *et al.*, 2006a; Popova *et al.*, 2010, 2012; Zhang *et al.*, 2010; Jin *et al.*, 2012, 2016]. The sea ice loss and early ice retreat also may affect the phenology (timing) of primary production and cause earlier phytoplankton blooms [Kahru *et al.*, 2011; Ji *et al.*, 2013]. Moreover, the changes in the lower trophic levels may have significant impacts on upper trophic levels [Wassmann *et al.*, 2006b; Loeng and Drinkwater, 2007]. As a consequence, shifts are occurring within the Arctic marine ecosystem across entire food webs, from phytoplankton, zooplankton, and benthos, to fishes, seabirds, and marine mammals [Grebmeier *et al.*, 2006; Wassmann, 2011, 2015].

Copepods of the genus *Calanus* play critical roles in the Arctic marine pelagic ecosystem. Four congeneric *Calanus* species coexist in the Arctic Ocean, including two endemics (*C. glacialis* and *C. hyperboreus*) and two expatriates (*C. finmarchicus* and *C. marshallae*) [Conover, 1988; Mauchline, 1998]. These copepods are key links between primary producers and large predators, transferring low-energy proteins and carbohydrates into high-energy lipids [Falk-Petersen *et al.*, 2009]. *Calanus* species usually dominate the mesozooplankton biomass in the Arctic/subarctic seas [e.g., Melle and Skjoldal, 1998; Ashjian *et al.*, 2003; Kosobokova

and Hirche, 2009; Hopcroft et al., 2010; Darnis and Fortier, 2014] and are high-quality food for the commercial fish species such as pollock, cod, capelin, and herring [Hunt et al., 2002; Wassmann et al., 2006b].

The endemic calanoid *C. glacialis* is the most important species of this genus in the Arctic shelf/slope seas [Falk-Petersen et al., 2009]. The life span of *C. glacialis* varies from 1 to 3 years, with a 2 year life cycle being most commonly observed [e.g., Smith, 1990; Slagstad and Tande, 1990; Madsen et al., 2001; Ashjian et al., 2003; Daase et al., 2013]. This species is well adapted to the strong seasonality of the Arctic environment and to pulsed food events from ice algal and pelagic phytoplankton blooms [Søreide et al., 2010; Leu et al., 2011]. In the springtime, female adults fuel gonad maturation and egg reproduction by utilizing either consumed under-ice algae or their body lipid reserves [Kosobokova and Hirche, 2001; Wold et al., 2011; Daase et al., 2013]. During the spring/summer phytoplankton bloom, *C. glacialis* offspring feed on the pelagic phytoplankton and microzooplankton to develop and molt, gain body mass, and accumulate energy reserves, primarily wax esters [Wold et al., 2007; Søreide et al., 2008; Campbell et al., 2009]. Over the winter, the late copepodids usually undergo a long period of dormancy (diapause) by descending to the deep water, reducing their metabolism, and subsisting on stored lipid reserves, presumably in order to survive starvation and/or predation [Runge et al., 1985; Kosobokova, 1999]. Copepodids must mature to the diapausing stage (C4 for *C. glacialis*) and accumulate sufficient lipid stores before the end of their growth season in the previous spring/summer in order to successfully overwinter and survive.

Understanding and predicting responses of planktonic communities to the changing physical and biological environments from a pan-Arctic perspective is very challenging because few long-term, high-frequency, and broad spatial coverage observations from the extreme Arctic Ocean exist [Wassmann, 2011, 2015]. Marine ecological models, particularly individual-based models (IBMs) that deal with organisms at the individual level and account for individuals' life history and/or behaviors, have proven to be useful tools in explaining observed biogeographic and ecological patterns across the entire Arctic Ocean [e.g., Ji et al., 2012] or in specific Arctic/subarctic seas [e.g., Berline et al., 2008; Maps et al., 2011; Hjøllø et al., 2012; Elliott, 2015; Kvile et al., 2016].

Earlier modeling work, an IBM coupled to physical model that provided ocean velocities and water temperature, by Ji et al. [2012] confirmed the importance of environmental seasonality and copepod life cycles in controlling the biogeography of the four *Calanus* species. However, the role of food availability in development could not be well addressed in that study because of the limited spatiotemporal resolution of satellite-based chlorophyll (food) estimation that was used to provide food to the IBM and the inability of satellites to estimate chlorophyll in ice-covered areas and in subsurface layers. Food limitation has been found to significantly prolong copepod development time in many laboratory calanoid copepod experiments [e.g., Campbell et al., 2001; Cook et al., 2007; Daase et al., 2011; Jung-Madsen and Nielsen, 2015]. Parameterizing food limitation in addition to temperature-dependent copepod life history development is a critical improvement over the work of Ji et al. [2012], since primary production and consequently phytoplankton food availability in the Arctic Ocean are extremely variable both spatially and temporally [e.g., Arrigo and van Dijken, 2011; Daase et al., 2013; Ji et al., 2013]. The Ji et al. [2012] study also was based on climatological-mean modeled environmental conditions rather than on modeled individual years.

Our overarching questions are: (1) How does the biogeography of the copepod *C. glacialis* respond to the ongoing environmental changes in the Arctic Ocean, particularly early ice retreat, ocean warming, and changes in primary production; (2) What are the specific roles of temperature and food in shaping *C. glacialis* biogeographic distribution and inducing its boundary shifts? Two contrasting years in the 2000s were chosen to conduct comparative numerical experiments through modeling life history development of *C. glacialis* individuals. Key environmental and life history traits, including temperature, food availability, reproduction timing, critical development time, and growth season length, were analyzed to explain modeled biogeographic distributions under various scenarios. Model sensitivity to food dependency was assessed. The modeled biogeographic zones for *C. glacialis* and typical environmental and life history traits were also summarized.

2. Materials and Methods

The basic approach was to offline couple an Arctic copepod individual-based model (ArclIBM) with a fully validated 3-D ice-ocean-ecosystem model that provided continuous pan-Arctic coverage of temperature,

food, and flow fields. These variables were averaged over the upper 60 m or from the ocean surface to bottom where depth is shallower than 60 m, or approximately the polar mixed layer [Bates *et al.*, 2005; Peralta-Ferriz and Woodgate, 2015]. This depth interval coincides with typical depths over which high abundances of *C. glacialis* reside and actively feed during the growth season [e.g., Ashjian *et al.*, 2005; Kosobokova and Hopcroft, 2010]. These depth-averaged velocity, temperature, and phytoplankton biomass concentration were then utilized to calculate physical advection and life stage progression. The trajectory (through horizontal advection) and accompanying temperature- and food-dependent development of an individual model copepod from each starting location was modeled; population size and success was not modeled. Each model simulation was run for the year of interest to identify locations where copepod individuals could successfully develop to the diapausing stage before overwintering.

2.1. Biophysical Model

Ocean circulation, water temperature, and upper water column phytoplankton concentrations were generated by the fully validated 3-D pan-Arctic Biology-Ice-Ocean Modeling and Assimilation System (BIOMAS) [Zhang *et al.*, 2010, 2014, 2015]. The model's generalized orthogonal curvilinear mesh covers the northern hemisphere north of 39°N, with the "north pole" of the mesh displaced into the land of Alaska to avoid singularity at the geographic North Pole [Zhang *et al.*, 2015]. North of 65°N latitude, the horizontal resolution ranges from approximately 4 km in the Bering Strait to 100 km in the Barents Sea. The model employs a Z-coordinate configuration in the vertical direction, with 30 ocean layers of varying thicknesses. The top six layers have a fine resolution of 5 m and the upper 100 m (approximate depth of euphotic zone) has a total of 13 layers, in order to better resolve the mixed layer and euphotic zone. Model mesh and vertical grid are shown in Supporting Information Figure S1.

Submodel components for ocean circulation, sea ice, pelagic ecosystem, and sea ice algae are online coupled in BIOMAS. The model is forced by the National Center for Environmental Prediction (NCEP)/National Center for Atmospheric Research (NCAR) reanalysis data that includes surface air temperature, specific humidity, cloudiness, precipitation, evaporation, surface wind, and downwelling shortwave radiation [Kalnay *et al.*, 1996]. The model also assimilates satellite observations of sea ice concentration [Lindsay and Zhang, 2006] and sea surface temperature [Manda *et al.*, 2005]. BIOMAS has been calibrated and validated using in situ and satellite observations of physical and biological variables (e.g., sea ice extent, ice edge, ice draft, snow depth, nitrate, primary productivity, chlorophyll-a concentration, and zooplankton biomass) [Zhang *et al.*, 2010, 2014, 2015]. It has also been used in model intercomparison studies and showed good agreements with other biogeochemical models [Popova *et al.*, 2012; Jin *et al.*, 2016]. Here model concepts and basics of the four submodel components are only briefly described.

The ocean circulation model is based on the Parallel Ocean Program (POP) developed at Los Alamos National Laboratory [Smith *et al.*, 1992]. The POP ocean model is modified by Zhang and Steele [2007] so that open boundary conditions can be specified. This allows one-way nesting of BIOMAS onto a global ice-ocean coupled model [Zhang, 2005] and imposes ocean velocity, temperature, salinity, and sea surface height at the southern boundaries along 39°N as open boundary conditions [Zhang *et al.*, 2015].

The sea ice model is a multicategory thickness and enthalpy distribution (TED) model, which utilizes a tear-drop viscous-plastic rheology and a line successive relaxation method to solve the ice momentum equation [Zhang and Hibler, 1997; Zhang and Rothrock, 2003]. A snow model is coupled into the sea ice model to calculate snow depth [Zhang *et al.*, 1998].

The lower trophic-level ecosystem model is adapted to the Arctic Ocean on the basis of an 11-component nutrient-phytoplankton-zooplankton (NPZ) biogeochemical model [Kishi *et al.*, 2007]. This pelagic ecosystem model consists of two phytoplankton components (diatom and flagellate), three zooplankton components (microzooplankton, mesozooplankton, and predator zooplankton), dissolved organic nitrogen, detrital particulate organic nitrogen, particulate organic silica, nitrate, ammonium, and silicate [Zhang *et al.*, 2010, 2014, Figure 3]. Nitrogen is utilized as the model currency, and all biogeochemical variables except particulate organic silica and silicate are expressed in mmol N m^{-3} ($1 \text{ mmol N m}^{-3} = 1.6 \text{ mg Chl-a m}^{-3}$ [Lavoie *et al.*, 2009]).

The sea ice algae component simulates algal colonies in the bottom 2 cm ice layer and is coupled to the pelagic ecosystem model through nutrient and biotic exchanges at the ice/ocean interface following Jin *et al.* [2006, 2012]. It has two ice algal components (diatom and flagellate), with nitrate, ammonium, and

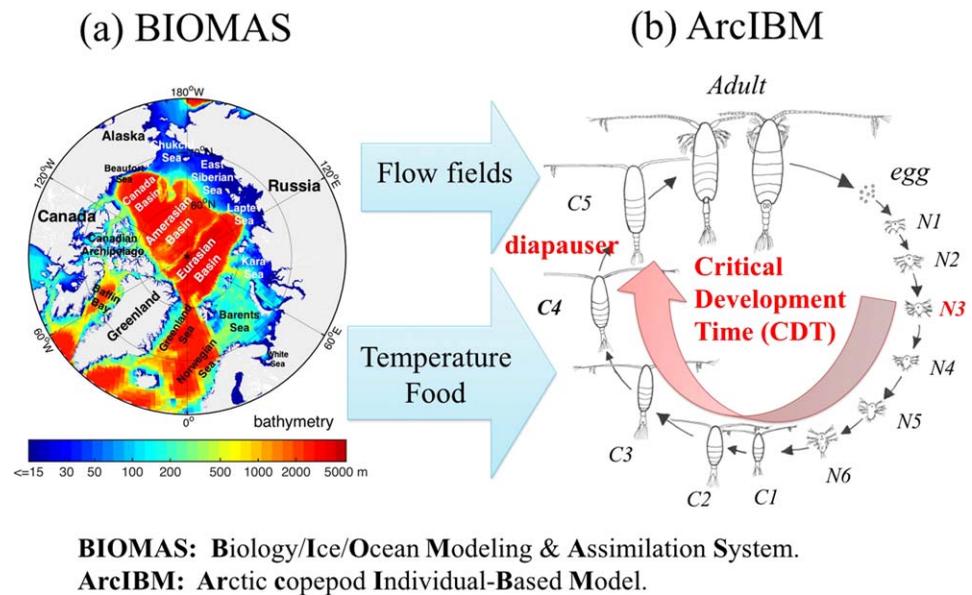


Figure 1. The offline model coupling between BIOMAS and ArcIBM. The BIOMAS-simulated daily-mean flow fields are temporally and spatially interpolated in ArcIBM to obtain meridional and zonal velocities for Lagrangian tracking. Temperature and food are interpolated to calculate copepod life history development. (a) The Arctic Ocean geography and BIOMAS bathymetry. The color bar illustrates bathymetry between 15 and 5000 m. Note that the minimum depth of the BIOMAS model grid is 15 m, equivalent to a minimum of three vertical layers. (b) Thirteen life stages of *C. glacialis*. N3 is the first feeding stage that food is required for life stage development, and C4 is the first diapausing stage for *C. glacialis*. The critical development time is defined as the time period required for *C. glacialis* to develop from the beginning of N3 to the midway between C4 and C5 (diapause).

silicate as limiting nutrients for ice algal growth. The ice algae and pelagic ecosystem models do not distinguish between ice and water column diatom (or flagellate) species.

Daily mean BIOMAS output variables, including meridional (positive northward) and zonal (positive eastward) current velocities (in m s^{-1}), ocean temperature (in $^{\circ}\text{C}$), and phytoplankton biomass concentration (summation of flagellate and diatom concentrations in mmol N m^{-3} as copepod food), were averaged over the upper 60 m and temporally and spatially interpolated to obtain input variables to update individual copepods' locations, ages, and life stages in the ArcIBM through a one-way offline coupling (Figure 1 and see Figure S2 for temporal and spatial interpolation schemes). Food dependency in copepod life stage development of the ArcIBM included both sea ice algae that are released from the ice to the water column and pelagic phytoplankton that grow in the upper euphotic zone, and assumed that copepods only utilize algal food in the water column with no dietary preference for flagellates versus diatoms (see section 2.2). Note that the mesozooplankton group in the BIOMAS has no direct relationships with the copepod individuals in the ArcIBM and zooplankton variables from BIOMAS are not utilized in the ArcIBM, although within the BIOMAS, mesozooplankton do impact the water column phytoplankton through grazing.

The BIOMAS-simulated upper ocean temperatures and phytoplankton biomass concentrations are examined briefly in Supporting Information Text S1, along with the sea ice conditions that are unique to the Arctic system and influence heat, light, and momentum transfers from the atmosphere to the ocean [Zhang et al., 2010, 2015]. The sea ice concentrations, ocean temperatures, and phytoplankton biomass concentrations in spring and summer months from May to August, largely overlapping with *C. glacialis* growth season, are presented in Figures S3–S5.

2.2. Copepod Individual-Based Model

The ArcIBM is a modified version of a generic Lagrangian tracking and zooplankton life-stage-based biological model [Ji et al., 2012]. The basic functionality evolves copepods both physically (i.e., advection) and biologically (i.e., aging, maturation, and life stage development) through time. The model source code was written using standard Fortran 90 language and is publicly available from the GitHub (<https://github.com/zfengwhoi/fiscm/tree/master/ArcIBM>).

The Lagrangian tracking module solves the following advection equation through a fourth-order Runge-Kutta (RK-4) scheme:

$$d\vec{x}(t)/dt = \vec{v}(\vec{x}, t), \quad (1)$$

where \vec{x} is the individual position vector (i.e., longitude and latitude) at time t and \vec{v} is the horizontal velocity vector linearly interpolated from the upper 60 m depth-averaged current velocities provided by BIOMAS. All model runs were configured in a 2-D horizontal mode, and therefore depth and vertical velocity were not used (BIOMAS vertical velocities are very small).

The biological module calculates copepod aging and life stage evolution throughout the entire life cycle of 13 stages, including egg, 6 nauplii ($N1$, $N2$, $N3$, $N4$, $N5$, and $N6$), and 6 copepodids ($C1$, $C2$, $C3$, $C4$, $C5$, and adult) (Figure 1b). Each copepod individual can be represented by a state vector (S), consisting of state variables such as locations (longitude and latitude), zonal (u) and meridional (v) depth-averaged velocity, temperature, and food concentration at the corresponding location, morphological stage (referred to as i -stage in Metz and Diekmann [1986]), and relative age within a stage (i.e., a decimal number that indicates progression from one stage to the next; for instance, an individual with $2.0 \leq \text{age} < 3.0$ is in stage $N1$). At the beginning of a model run, each individual was initialized with a starting location, stage, and age. Then corresponding horizontal velocities, temperature, and phytoplankton biomass concentration (i.e., food) were linearly interpolated from the external BIOMAS forcing to advect the individuals every 10 min (physical time step) and age (develop) them hourly (biological time step).

Both temperature and food availability determine development time and rate in copepods, with life stage development being significantly prolonged under food limitation [Campbell et al., 2001; Cook et al., 2007; Daase et al., 2011; Jung-Madsen and Nielsen, 2015]. Here age was updated using temperature- and food-dependent development rate derived from Belehrádek [1935] and Ivlev [1955] functions with coefficients fitted to the laboratory data. Under food saturation, the development time D_i (days) at the i th stage (or stage duration) can be expressed as

$$D_i = a_i(T + \alpha)^\beta, \quad (2)$$

where a_i and α are fitting parameters, T is temperature (in °C), and β is a constant for a range of copepod species [Corkett et al., 1986; Campbell et al., 2001; Jung-Madsen and Nielsen, 2015]. The derivations of the above parameters can be found in Ji et al. [2012] and all parameters are listed in Supporting Information Table S1.

Food dependency is applied to equation (2) starting with the first feeding naupliar stage $N3$ using a factor of the Ivlev function [Ivlev, 1955] in the denominator, similarly to other stage-based models [Speirs et al., 2005, 2006; Ji et al., 2012]

$$D_i = \begin{cases} a_i(T + \alpha)^\beta, & i=1, 2, 3 \\ a_i(T + \alpha)^\beta / (1 - e^{-F/K}), & i=4, 5, \dots, 12 \end{cases}, \quad (3)$$

where F is phytoplankton food concentration (in mmol N m^{-3}), K is a food-limitation parameter (in mmol N m^{-3}), and i is the life stage number. Nitrogen-based food concentration was used in order to be consistent with the BIOMAS forcing. The K value of $0.5 \text{ mmol N m}^{-3}$ (or equivalent to 39.8 mg C m^{-3} using the Redfield C-N ratio of 106:16 [Redfield et al., 1963]) was fitted to the development rate measurements of laboratory-reared *C. finmarchicus* [Campbell et al., 2001] (see Figure 2a) and represents a best-case estimation. Carefully controlled growth and development studies have not been conducted for *C. glacialis*, as they have for *C. finmarchicus*. The intergeneric equiproportional rule [Hart, 1990] has been applied to estimate stage durations for *C. glacialis* based on the limited data on development for this species and the equations describing development from the *C. finmarchicus* study. The two species are closely related, have similar life cycle strategies, and may interbreed in regions where they overlap significantly (e.g., Gulf of St. Lawrence [Parent et al., 2012]).

Finally, the development rate R_i (day^{-1}) is a reciprocal of the development time (Figure 2b):

$$R_i = \begin{cases} 1/[a_i(T + \alpha)^\beta], & i=1, 2, 3 \\ (1 - e^{-F/K})/[a_i(T + \alpha)^\beta], & i=4, 5, \dots, 12 \end{cases}. \quad (4)$$

The dimensionless food-limitation factor $(1 - e^{-F/K})$ is sensitive to the food concentration in the range from 0.005 to $2.3 \text{ mmol N m}^{-3}$. When calculating the development rate, an uppermost limit (i.e., saturation) was

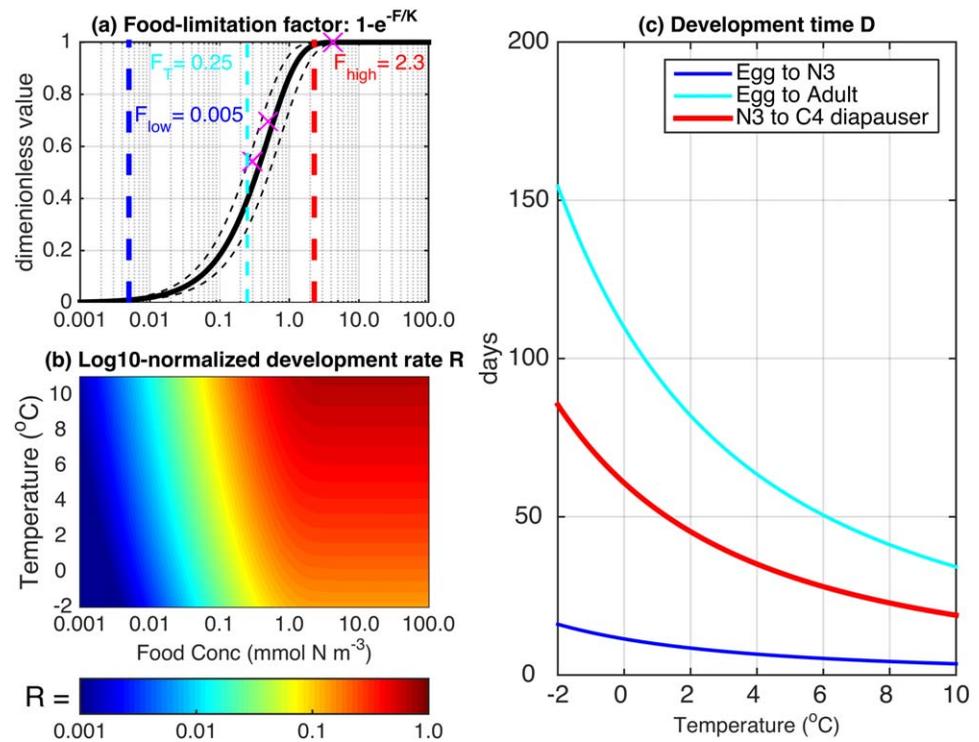


Figure 2. Temperature- and food-dependent life history development of *C. glacialis* based on Belehrádek and Ivlev functions. (a) Food-limitation factor, which indicates a fraction of the maximum development rate at a certain temperature when food becomes limited, is an Ivlev function of nitrogen-based food concentration (see equation (4)). The black solid curve illustrates the functional response for K value of $0.5 \text{ mmol N m}^{-3}$ that is fitted to the laboratory data (magenta crosses) of Campbell *et al.* [2001], in which three food levels each with two replicates were maintained for a growth and development study with *Calanus finmarchicus* at 8°C . Two black dashed curves illustrate the functional responses for K values of 0.25 and $0.1 \text{ mmol N m}^{-3}$ used in the model sensitivity runs (see section 2.3.7). The red and blue vertical lines mark food saturation threshold and starvation concentrations. The cyan line marks a low-food threshold of $0.25 \text{ mmol N m}^{-3}$, below which life stage development is suspended in the low-food-threshold runs (see section 2.3.7), and is also used to calculate growth season end (see section 2.3.2). (b) Log₁₀-normalized development rate R (day^{-1}) as a function of food and temperature. For contour plotting, a normalization coefficient ($a_n = 1000$) is used, and the actual development rate at the i th stage can be obtained by multiplying a ratio of a_n/a_i (see equation (4) and Table S1). (c) Development time under food saturation through first three nonfeeding stages (egg to N3), the whole life cycle (egg to adult), and the critical development time, required for *C. glacialis* to develop from the beginning of N3 to midway between C4 and C5.

set at $2.3 \text{ mmol N m}^{-3}$, above which food becomes saturated and life stage development is only temperature-dependent. This saturated food concentration corresponds to the concentration where development rate reaches 99% of its maximum at a certain temperature (Figure 2a). The lowermost limit (i.e., starvation) of $0.005 \text{ mmol N m}^{-3}$ corresponds to 1% of the maximum development rate. Since early life stages from egg to N2 are nonfeeding stages, stage development in these three stages is independent of food (see equation (4)).

The transition time through the first three nonfeeding naupliar stages is much shorter than the time for later life stages during which *C. glacialis* requires food. According to equation (3), the maximum time required for *C. glacialis* to develop from egg to the beginning of N3 is approximately 2 weeks (15.5 days) at the ocean freezing temperature (-1.8°C). Under saturated food, the critical development time, required for *C. glacialis* to develop from the start of N3 to mid-way through the first diapausing stage C4 [Ji *et al.*, 2012], is approximately 82 days at -1.8°C , 61 days at 0°C , and 45 days at 2°C (red curve in Figure 2c). When food is limiting, the critical development time can be substantially prolonged so that *C. glacialis* may not advance into the lipid-rich diapausing stage and subsequent overwintering is likely to fail.

2.3. Experimental Design

A series of numerical experiments were designed to address how early ice retreat and ocean warming may affect the timing of *C. glacialis* adult female reproduction, and subsequent development conditions (i.e., temperature and food) for *C. glacialis* offspring (Table 1). These factors further determine whether *C. glacialis*

Table 1. Numerical Experiments for Hypothesis and Sensitivity Tests

Scenario	Model Forcing	Key Assumption	Hypothesis
Baseline	Depth-averaged velocity, temperature, and phytoplankton food of the active layer (0–60 m)	The income breeders fuel egg reproduction and lay eggs at the onset of phytoplankton bloom	Ocean warming and early ice retreat may induce <i>C. glacialis</i> biogeographic boundary shifts by changing its growth start and length, and developmental conditions (temperature and phytoplankton food) in the growth season
Early reproduction	Same as baseline	The capital breeders fuel lipid-based egg reproduction prior to the onset of phytoplankton bloom	The lipid-based early reproduction leads to a perfect timing match between feeding-stage (<i>N3</i> and older stages) <i>C. glacialis</i> individuals and water column phytoplankton food
Food seeking	Same as baseline except food being maximum phytoplankton concentration of the active layer	The copepods are capable of vertically migrating to the depth of most abundant food supply	Adaptive behaviors are critical for <i>C. glacialis</i> to sustain populations in a deficient food environment (e.g., Arctic basins) and to cope with variations in the food supply from the primary production
Without food limitation	Same as baseline except always saturated food	Without food limitation, life stage development of <i>C. glacialis</i> is only temperature-dependent	The individuals only succeeding in the runs without food limitation reveal the biogeographic regions where <i>C. glacialis</i> is sensitive to the quantity of food during the growth season
Without ice algae	Temperature and velocity are the same as baseline but ice algae are turned off	Released ice algae in the water serve as early food in the growth season	Without ice algal food early in the growth season, those <i>C. glacialis</i> individuals require long critical development may not develop to successful diapausing stages
Sensitivity of food-limitation parameter <i>K</i>	Same as the baseline except doubling or halving <i>K</i> values	Food dependency is a major source of uncertainty in modeling copepod development	Despite uncertainties associated with food dependency, <i>C. glacialis</i> individuals in certain regions can develop to <i>C4</i> diapausers under a range of food-limitation parameter values
Sensitivity of low-food threshold	Same as the baseline except applying a low-food threshold to suspend stage development at the low-food range	Life stage development only occurs when food concentration exceeds a threshold to meet basal metabolic demand	This species is well adapted to the seasonality of the food supplies from the phytoplankton blooms. It primarily relies on the moderate to high food concentrations during the bloom period for life stage development

individuals attain the diapausing stage by the end of the growth season under various scenarios and suggest that potential biogeographic boundary shifts of this model species may occur under the changing environment (Table 1). Two contrasting years, 2001 (cold) and 2007 (warm), were chosen to model and to compare *C. glacialis* biogeographic distributions, because ocean surface warming and sea ice decline have been particularly pronounced since the early 2000s [Steele et al., 2008; Stroeve et al., 2012]. The cold and warm years may be thought of the “old” and “new normal” Arctic eras, respectively [Jeffries et al., 2013]. Environmental conditions (i.e., sea ice, temperature, and phytoplankton food) in both years were briefly described in Supporting Information Text S1. Model assumptions and implementations pertinent to numerical experiments in Table 1 were explained in details below.

2.3.1. Model Initialization

Under the assumption that *C. glacialis* adult females can reproduce offspring anywhere in the Arctic Ocean, 17,043 individual copepods were uniformly distributed every 0.25° great circle distance (~25 km) inside the 65°N circle (see Figure S6). Mortality was neglected in this study, both because ecological causes for observed mortality of *Calanus* copepods in the Arctic are still largely unknown [Daase et al., 2014] and because the goal was to identify locations where an individual could successfully diapause based on given environmental conditions rather than to model population size. This simplification implies that the model experiments were restricted to the bottom-up processes that are regulated by variability in temperature and food availability, despite the potential importance of top-down control (e.g., predation) in the Arctic planktonic ecosystem [e.g., Berge et al., 2012; Varpe, 2012; Varpe and Fiksen, 2010; Varpe et al., 2015].

2.3.2. Growth Season, Potential Diapause, and Overwintering Success

All ArcIBM simulations were run from the beginning until the end of the calendar year. However, the copepod growth season is only a fraction of the year, mainly spring and summer, when phytoplankton food in the upper ocean is sufficient to support *C. glacialis* life stage development and lipid gain. In each simulation, all *C. glacialis* individuals were released at the onset of the phytoplankton bloom, or the copepod growth season start (Figures 3a and 3b). This time was determined by applying a cumulative sum method [Brody

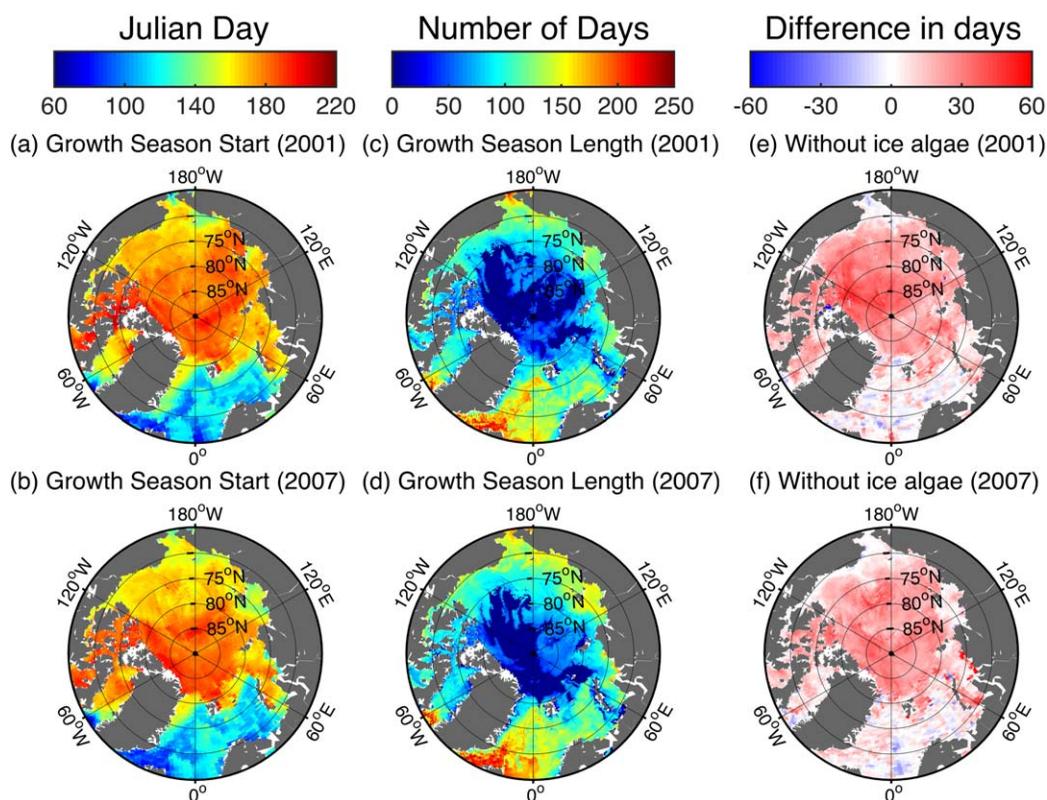


Figure 3. Growth season start time (left) and growth season lengths (middle) of all *C. glacialis* individuals in the baseline runs, and changes of growth season start in without-ice-algae runs (right) compared to the baseline runs. The growth season starts are equivalent to the onset of phytoplankton bloom. All individuals are positioned at their release locations.

et al., 2013] to the upper 60 m depth-averaged phytoplankton concentrations (see Supporting Information Text S2). The end of the growth season for each individual was set at the time when phytoplankton food dropped below a low-food threshold. This threshold can be calculated based on an energetic balance concept assuming a basal metabolic food requirement that must be exceeded to allow net lipid accumulation. The threshold value ($0.25 \text{ mmol N m}^{-3}$) was estimated from in situ feeding and respiratory experiments with *C. glacialis* during recent Bering/Chukchi Sea cruises [Campbell *et al.*, 2015; R. G. Campbell and C. J. Ashjian, unpublished data].

For each individual to survive overwintering, it must develop to past the midway point between the diapausing stages *C4* and *C5* to store sufficient lipids before the end of the growth season [Ji *et al.*, 2012]. During the postprocessing of model results, these individuals developing past half way of *C4* were categorized as successful diapausers. Conversely, the remaining individuals not attaining midway *C4* by the end of growth season are nondiapausers, which are less likely to survive overwintering due to insufficient lipid reserves. The Julian day and corresponding longitudinal and latitudinal locations at which *C. glacialis* individuals became *C4* diapausers were identified and regarded as potential diapausing initiation locations. The critical development time, required to develop from the first feeding stage *N3* to midway *C4*, was calculated for all successful diapausers. Finally, the geographic locations of all *C4* diapausers depict modeled biogeographic regions where *C. glacialis* is likely to recruit and establish viable populations and may indicate biogeographic boundary shifts of this species from year to year under various scenarios.

2.3.3. Experiment With Reproduction Timing

The reproduction of *C. glacialis* may be fueled by two distinctive strategies, either by utilization of internal lipid reserves (capital breeding) or by uptake of external food (income breeding) [Wold *et al.*, 2007; Daase *et al.*, 2013]. This mixed reproductive strategy improves this species' plasticity and fitness to the narrow growth season that is comprised of short and intense food supplies from ice algal and phytoplankton blooms [Varpe *et al.*, 2007, 2009; Sainmont *et al.*, 2014]. Most reproduction is accomplished by income

breeding with *C. glacialis* egg production dependent on available food [Hirche and Kattner, 1993; Plourde et al., 2005; Wold et al., 2011; Durbin and Casas, 2014].

The baseline runs in 2001 and 2007 were designed by assuming income breeders lay eggs immediately after food becomes available in the water column. In the baseline runs, all *C. glacialis* individuals were initialized with egg and released at the onset of the phytoplankton bloom (Figures 3a and 3b). The available food at the onset of the bloom was composed mostly of released sea ice algae, consistent with prior field observations that found reproduction of *C. glacialis* occurred in advance of pelagic phytoplankton bloom [e.g., Smith, 1990; Tourangeau and Runge, 1991; Hirche and Kattner, 1993; Kosobokova, 1999; Kosobokova and Hirche, 2001; Hirche and Kosobokova, 2003; Søreide et al., 2010; Wold et al., 2011; Durbin and Casas, 2014].

To examine the impact of the timing of *C. glacialis* adult reproduction on the developmental success of their offspring, an early-reproduction scenario was designed by initializing individuals with the first feeding stage *N3* and also releasing them at the bloom onset (see Table 1 for early reproduction scenario). The *N3* initialization may represent lipid-based reproduction and can be regarded as a perfect timing match scenario so that the food requirement for copepod development is synchronized with the food availability from the phytoplankton bloom. This assumption implies that modeled individuals that reproduced as eggs prior to the bloom onset would halt at the beginning of *N3* until food emerges in the water column. The laboratory experiment supported that development of starved *C. glacialis* eggs/nauplii could arrest at stage *N3* for more than 1 month without significant mortality [Jung-Madsen and Nielsen, 2015].

2.3.4. Experiment With Food-Seeking Behavior

Food limitation was further explored by instituting a food-seeking behavior in which the copepods were assumed to migrate and feed at the depth of the maximum phytoplankton concentration in the upper 60 m (see Table 1 for food seeking scenario) within each 1 h biological time step and thus to develop using the elevated food availability, rather than to develop using the depth-averaged food concentrations as in the baseline scenario. The food-seeking implementation was partially supported by observations in the Chukchi Sea [Ashjian et al., 2005], northwest Barents Sea [Norrbin et al., 2009], Canada Basin [Kosobokova and Hopcroft, 2010], and Amundsen Gulf [Darnis and Fortier, 2014] that copepod population depth distributions and the subsurface chlorophyll maxima may be coincident. To isolate the effect of food quantity on *C. glacialis* development, depth-averaged temperatures and velocities were still used as in the baseline scenario and the growth season also remained the same.

2.3.5. Experiment Without Food Limitation

ArcIBM experiments without food limitation were conducted to disentangle the effects of temperature and food on *C. glacialis* development and biogeographic boundary shift (see Table 1 for without-food-limitation scenario). This implementation assumed that food is always saturated, so development is only temperature-dependent. All other variables, including initial release time, location and life stage, temperatures, and velocities, and the growth season remained the same as the baseline scenario.

2.3.6. Experiment Without Ice Algae

The consumption of ice algae by copepods has been confirmed by the presence of a large amount of ice algal diatoms inside the guts of *C. glacialis* in the northern Bering Sea during late winter [Durbin and Casas, 2014]. Ice algal blooms have three distinctive bloom phases: (1) a predominant heterotrophic prebloom phase with high snow cover and low light availability, (2) a bloom phase when penetrated sunlight supports high ice algal productivity, and (3) a postbloom phase that has a strong sympagic-pelagic-benthic coupling [Leu et al., 2015]. Sea ice algae probably fuels egg reproduction by female adults (income breeders) during the second phase, whereas the utilization of released ice algal food and pelagic phytoplankton in the water by young naupliar copepods most likely occurs in the third phase. In the ArcIBM, it was assumed that *C. glacialis* individuals can only feed on ice algae in the water together with pelagic phytoplankton, rather than while attached to the ice. To investigate the importance of released ice algae to *C. glacialis* development, ArcIBM experiments were run with ice algal submodel of BIOMAS turned off, resulting in water column food derived only from pelagic phytoplankton rather than from a combination of released ice algae and phytoplankton (see Table 1 for without-ice-algae scenario).

2.3.7. Model Sensitivity Analyses

Food dependency may be the largest source of uncertainty in modeling *C. glacialis* life history development. Development rate experiments with *C. glacialis* are very few so that parameterization of the temperature- and food-dependent development rates mainly relied on the knowledge of its congener, *C. finmarchicus*, and on the intergeneric equiproportionality of calanoid copepod development [Hart, 1990; see Ji et al.,

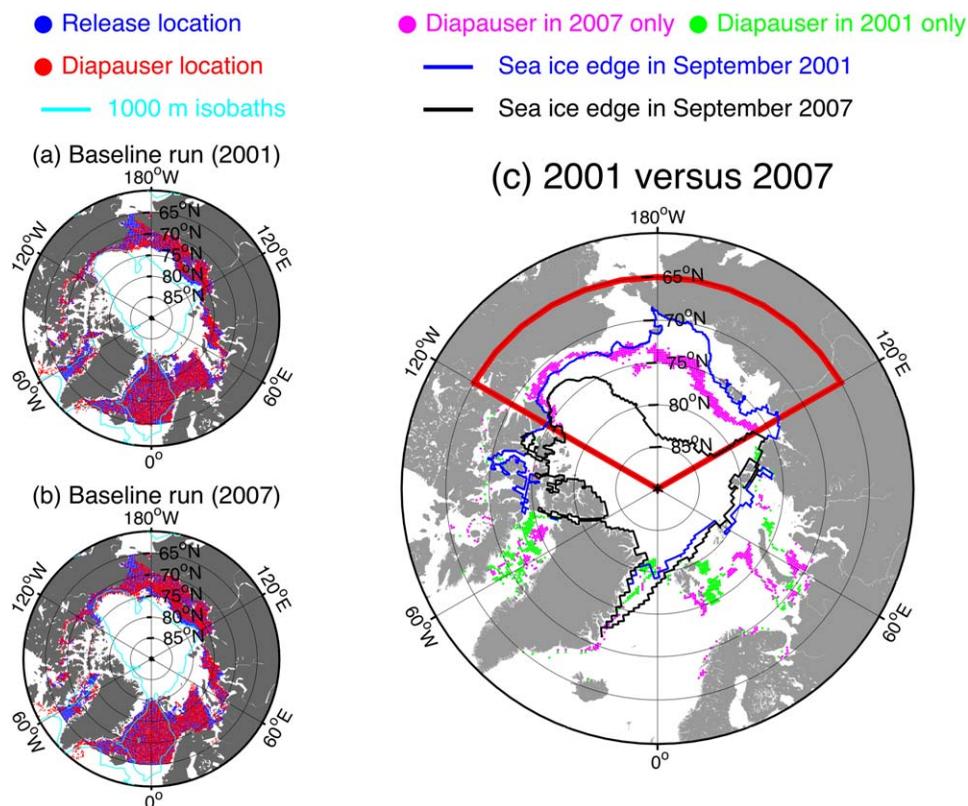


Figure 4. Model results of successful diapausing *C. glacialis* individuals in the baseline runs: (a) 2001, (b) 2007, and (c) 2001 versus 2007. In the left two figures, blue and red dots represent initial release locations and final locations of *C4* diapausers, respectively (nondiapauser individuals in the central blank regions are not shown). The cyan lines are 1000 m isobaths, which divide Arctic shelf/slope seas with deep basins. In the right panel, magenta and green dots are exclusive diapausers in 2007 and 2001 only (common diapausers in both years are not shown). The model-simulated minimal sea ice edges in September 2001 and 2007 are illustrated by blue and black lines. The ice edge is the outer boundary of ice extents, or areas with monthly-mean ice concentrations higher than 15%. The red fan zone contains the Pacific Arctic seas where northward expansion of *C. glacialis* biogeographic boundaries occurred in 2007. For direct comparisons of the same individuals among different years, all individuals in Figure 4c are positioned at their identical release locations in both years.

2012 for details]. Also, the value of the food-limitation parameter K was fitted to only three levels of controlled food conditions at a constant temperature of 8°C (see equation (4) and Figure 2a) and the same laboratory study showed increased variability in the development rate and less certainty in the stage duration estimations under medium to low food treatments [Campbell *et al.*, 2001].

Two types of sensitivity analyses were performed in order to examine whether changing food dependency will dramatically affect modeled distributions of *C. glacialis* diapausers (Table 1). The first set of experiments simply varied the food-limitation parameter K . Increasing (or decreasing) K values indicates life stage development being more (or less) dependent on food concentrations (see Figure 2a). Two sensitivity runs using doubled and halved K values were conducted. The second set of experiments applied a low-food threshold, below which development rate is zero and stage development is arrested. The same threshold value ($0.25 \text{ mmol N m}^{-3}$) based on the metabolic energetics theory (see section 2.3.2) was utilized in the low-food-threshold runs.

2.3.8. Categorization of Arctic Ocean Regions Based on Modeled *C. glacialis* Biogeography

Daase *et al.* [2013] synthesized available observations at various study sites and summarized three paradigms of mixed life history traits reflected in *C. glacialis* adaptation to the highly variable Arctic environments in three regions: (1) long-lasting ice-covered regions, where female adults utilize the spring ice algal bloom for reproduction and their progeny subsequently feed on the summer pelagic bloom; (2) open shelf/slope seas that are impacted by warmer water inflows (from Atlantic or Pacific), where ice and primary production timing varies; (3) open water regions with no or very limited ice cover and only one spring bloom. This type of categorization provided a useful framework to understand life history traits that structure the biogeography of this species. Here the Arctic Ocean regions were categorized

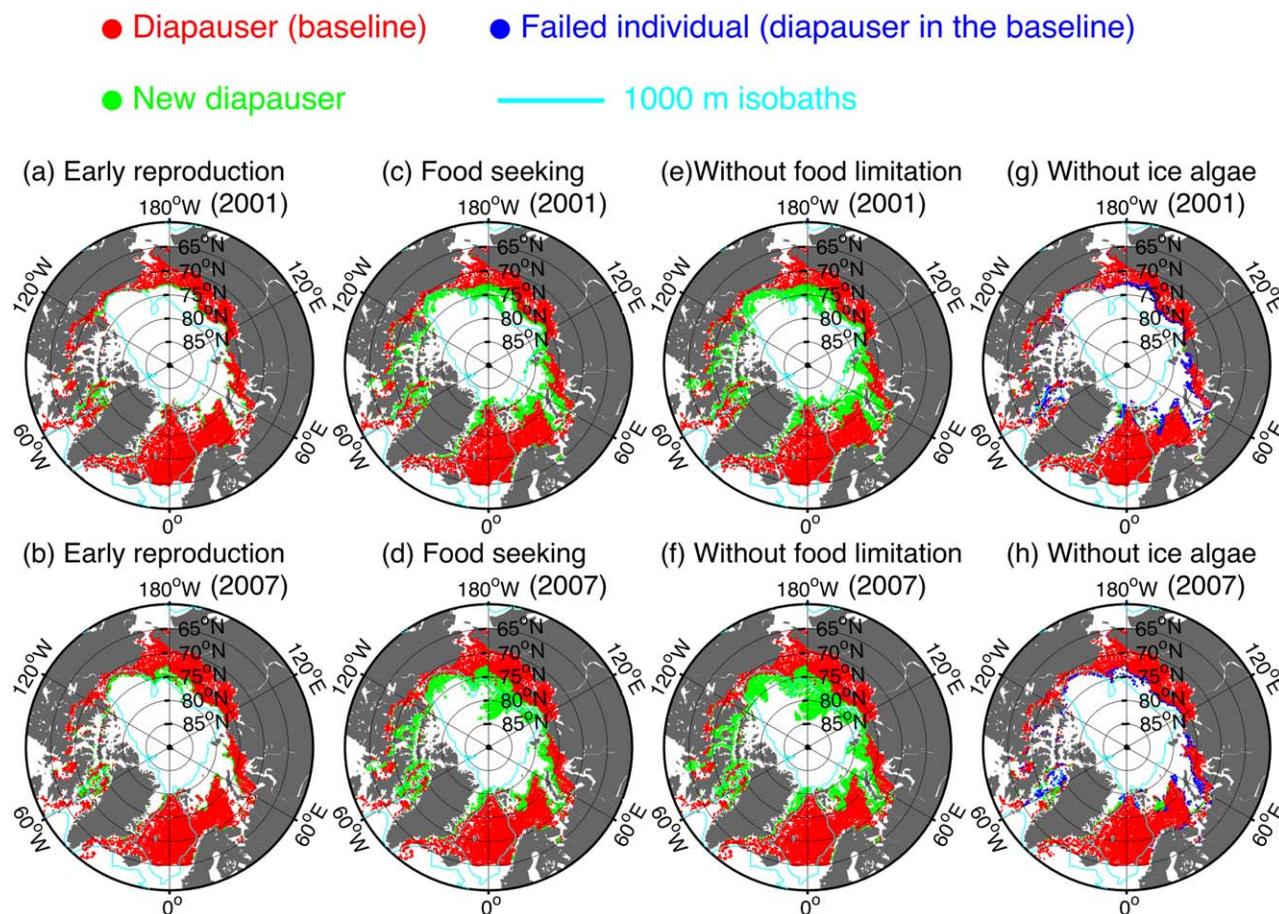


Figure 5. Additional model runs for early reproduction, food-seeking, without-food-limitation, and with-ice-algae scenarios. The same diapausers in these scenarios as in the baseline runs (Figures 4a and 4b) are illustrated in red dots. The green and blue dots show new diapausers (nondiapausers in the baseline runs) and failed nondiapauser individuals in these scenarios (diapausers in the baseline runs). The initial release locations of the individuals are not shown. See Table 1 for experimental designs.

into five biogeographic zones, based on the present modeling study of *C. glacialis* life history development (see section 3.4).

3. Results

3.1. Biogeographic Distributions of *C. glacialis* Diapausers in 2001 Versus 2007

Model results showed both similarities and discrepancies between the two modeled years in *C. glacialis* diapauser distributions, demonstrated by the two baseline runs (Figure 4). Notably, *C. glacialis* individuals could not develop to diapausers over the vast majority of the central Arctic basins (deeper than 1000 m isobaths; see cyan lines in Figures 4a and 4b) in both years and so were unlikely to establish self-sustaining populations. The individuals that spawned inside the 80°N circle rarely became C4 diapausers by the end of growth season (Figures 4a and 4b). Overall, *C. glacialis* could thrive only in the subarctic seas, along the Arctic shelves and adjoining slope seas, and in the Baffin Bay and southern Canadian Arctic Archipelago. The modeled distribution patterns agreed with the established understanding of the distribution of this Arctic endemic copepod species that *C. glacialis* is a cold-water shelf/slope species with low abundances in the deep basins [e.g., Ashjian et al., 2003; Hirche and Kosobokova, 2003; Hopcroft et al., 2005; Kosobokova and Hirche, 2009].

Major differences in the biogeographic distributions of *C. glacialis* diapausers between the two study years were found in the Pacific Arctic sector, specifically along the Beaufort, Chukchi, East Siberian, and Laptev Seas (see Figure 4c magenta dots in the red fan zone). In 2001, the northern boundaries of the C4 diapausers aligned with the 1000 m isobaths in the Beaufort Sea and much further south of that isobath in the

Table 2. Number (and Percent Change) of *C. glacialis* Individuals Successfully Developing to C4 Diapausers in the Baseline and Other Scenarios^a

Scenario ($n_{total} = 17,043$)	Pan-Arctic		North of 70°N	
	Year 2001	Year 2007	Year 2001	Year 2007
Baseline	7,317	7,810	4,856	5,382
Early reproduction	7,760 (+6.0%)	8,377 (+7.3%)	5,212 (+7.3%)	5,844 (+8.6%)
Food seeking	9,621 (+31.5%)	10,532 (+34.9%)	6,914 (+42.4%)	7,882 (+46.5%)
Without food limitation	10,377 (+41.8%)	11,490 (+47.1%)	7,580 (+56.1%)	8,772 (+63.0%)
Without ice algae	6,777 (-7.4%)	7,480 (-4.2%)	4,295 (-11.6%)	5,088 (-5.5%)

^aThe percentage changes in the scenarios are normalized by the numbers of diapausers in the baseline runs of the corresponding year. The north of 70°N individuals are counted using individuals' geographic latitudes where they attain C4 diapausers.

Chukchi, East Siberian, and Laptev Seas. By comparison, in 2007, *C. glacialis* extended its northern boundaries by a few degrees of latitude further into the slope seas and into the fringe of the Canada Basin. The poleward expansion of successful *C. glacialis* diapausers coincided with dramatic losses of sea ice in 2007 compared to 2001, as indicated by the minimal sea ice edges of the two years (Figure 4c).

3.2. Distribution of *C. glacialis* Diapausers Under Various Scenarios

The early reproduction scenario, which initialized *C. glacialis* individuals with stage N3 instead of the egg stage, did not significantly change the overall biogeographic distributions of C4 diapausers by the end of the growth season (Figures 5a and 5b). If reproduction, presumably fueled by body lipids, occurred earlier than in the baseline runs, 6.0 and 7.3% more *C. glacialis* individuals became diapausers in 2001 and 2007, respectively (Table 2). This suggested that the plasticity of this species allows adaptation and recruitment despite variations in reproduction timing. Those individuals most susceptible to the timing changes resided on the northern boundaries of the modeled distribution and in some parts of the Baffin Bay (green dots in Figures 5a and 5b).

Including food-seeking behavior so that *C. glacialis* developed using optimal food conditions (i.e., maximum phytoplankton food of the upper 60 m) allowed it to dramatically expand its northern limits beyond the geographic regions achieved in the baseline runs to previously unsuccessful territories, such as the mid Canadian Archipelago, East Greenland Shelf, northern Barents Sea, and a small portion of the central basins (Figures 5c and 5d). In this scenario, 30–35% more *C. glacialis* individuals developed to C4 diapausers in the two study years (Table 2).

By assuming food is always saturated but by keeping the growth season length unchanged, 40–50% more *C. glacialis* individuals became diapausers by the end of the growth season (Table 2). The *C. glacialis* individuals at latitudes north of 70°N were even more dependent on available food than at more southern locations, with 56.1 and 63.0% more individuals successfully developing to diapausers in the 2001 and 2007 without-food-limitation runs (Table 2). The distributions of diapausers in the without-food-limitation runs (Figures 5e and 5f) were similar to those in the food-seeking runs (Figures 5c and 5d).

Turning off ice algae in the BIOMAS forcing primarily delayed the emergence of water column (here phytoplankton) food and, consequently, the copepod growth season start (Figures 3e and 3f; also see Figure S7). Such a delay was much more prominent in the perennially ice-covered central basins than in the open-water Norwegian Sea. Turning off ice algae had little impact on the overall distributions of *C. glacialis* diapausers (Figures 5g and 5h). However, without the ice algal food released to the water column during the early phase of the growth season, some *C. glacialis* individuals living in the northern boundaries could not develop to successful diapausers (blue dots in Figures 5g and 5h), with 7.4 and 4.2% fewer individuals succeeding in 2001 and 2007, respectively (Table 2).

3.3. Model Sensitivity Analyses

Only individuals in the northern boundaries of the modeled biogeographic distributions were sensitive to the food-limitation parameter *K* in the range between twice and half of the fitted *K* value (Figures 6a–6d). With greater food dependency (doubled *K*), *C. glacialis* diapausers were limited to the inner shelves, southern Baffin Bay, and southern Canadian Archipelago, as well as the open water Norwegian and Greenland Seas (Figures 6a and 6b). By comparison, diapausers became more widespread along the Arctic shelf/slope seas in the simulations using a halved food limitation parameter *K*, although central basin individuals were

● Diapauser (baseline) ● Failed individual (diapauser in the baseline)
 ● New diapauser — 1000 m isobaths

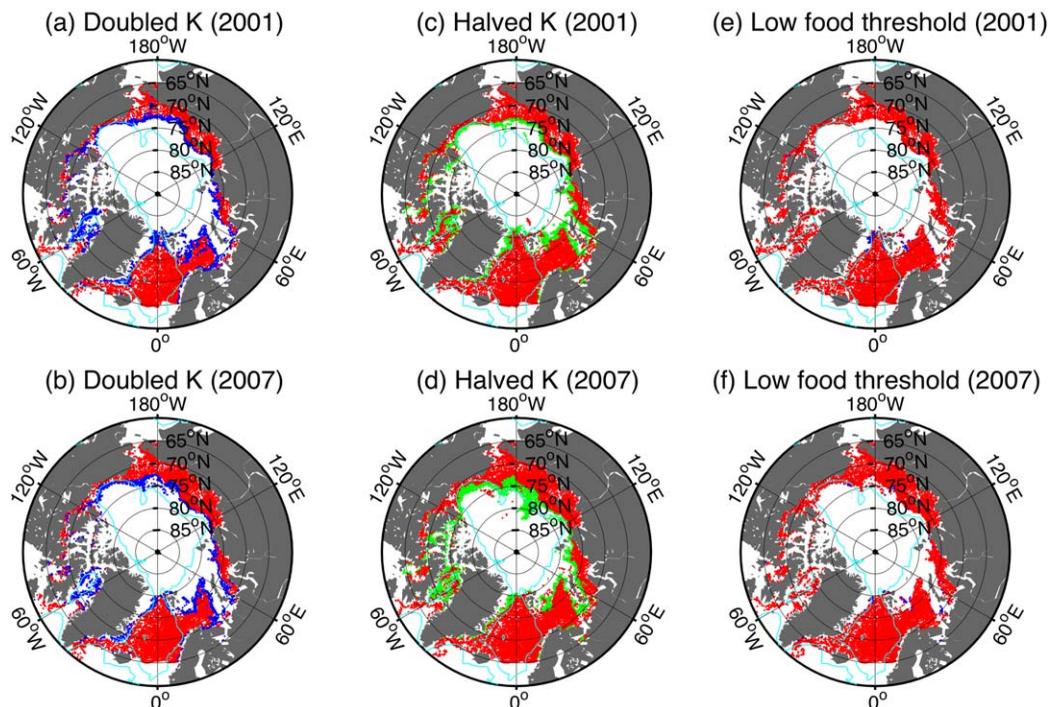


Figure 6. Model sensitivity runs showing distributions of *C4* diapausers in the scenarios of doubled food-limitation parameter *K* (more food-dependent), halved *K* (less food-dependent), and the low-food threshold. The same diapausers in these runs as in the baseline runs (Figures 4a and 4b) are illustrated in red dots. The green and blue dots show new diapausers (nondiapausers in the baseline runs) and failed nondiapauser individuals in these scenarios (diapausers in the baseline runs). See Table 1 for experimental designs.

still mostly unsuccessful even with reduced food dependency (Figures 6c and 6d). Also, applying the low-food threshold had little impact on *C. glacialis* diapausers' distributions in both 2001 and 2007 (Figures 6e and 6f). This suggested that most of the successful diapausers adapt to the seasonality of the phytoplankton blooms as they rely on the moderate to high food concentrations that exceed the set threshold value for their life stage development.

Table 3. Five Typical *C. glacialis* Biogeographic Zones Summarized From the Pan-Arctic Individual-Based Modeling of Its Life History

	Zone 1	Zone 2	Zone 3	Zone 4	Zone 5
Critical development time	Short (<45 days)	Long (>90 days)	Intermediate (45–90 days)	Intermediate (45–90 days)	Fail to develop to <i>C4</i> diapausers
Reproduction timing	Relatively early (spring)	Relatively late (summer)	Variable	Variable	Very late
Cumulative Food	Intermediate	Intermediate	High	Highly variable	Very low
Cumulative Temperature	High	Low	Variable	Highly variable	Very low
Environmental traits	Open water; warm water temperature; spring bloom	Long-lasting ice cover; summer bloom; ice algae food is critical	Intensive summer phytoplankton blooms occur after ice breakup	Both temperature and food have high spatiotemporal variability	Perennial ice and snow covers restrict light penetration and pelagic phytoplankton growth
Life history traits	1–2 year life cycle and may have a second generations if conditions permit	2–3 year life cycle	2 year life cycle	1–3 year life cycle	Cannot sustain viable populations due to low temperature and food and very short growth season
Geographic regions	Norwegian Sea	Slope seas between shelf seas and deep basins; eastern Greenland shelf; a portion of Baffin Bay	Shallow shelf seas including Beaufort, Chukchi, East Siberian, Laptev, and Kara	Regions other than Zones 1–3 and 5	Central Arctic basins; northern Canadian Archipelago

3.4. Typical Biogeographic Zones Revealed by Temperature, Food, and Critical Development Time

Four primary types of biogeographic zones in which *C. glacialis* individuals successfully developed and one biogeographic zone in which *C. glacialis* individuals could not develop to diapausers were identified, each with different combinations of critical development time, reproduction timing, and food and temperature regimes (Table 3). In essence, the relative lengths of the critical development time versus the growth season determine the developmental success or failure of the modeled *C. glacialis* individuals. A long critical development time indicates a slow maturation process due to very low temperature, scarce food, or a combination of both. Individuals with a critical development time longer than their growth season length would fail because they could not develop to the diapausing stages in one growth season. For example, basin-released *C. glacialis* individuals are unlikely to develop to C4 diapausers (see Figure 4 central blank regions) since their critical development time at these consistently low temperatures exceeded the time period during which adequate food was available (i.e., growth season). The relationship between temperature and food availability was explored by integrating daily temperature and food output over the critical development time to obtain cumulative temperature (CumT) and food (CumF) for each diapauser (Figure 7). These two variables represent the gross developmental conditions for *C. glacialis* diapausers. The critical development time, reproduction timing, growth season length, and cumulative temperature and food were utilized to partition the Arctic Ocean into multiple biogeographic zones (Table 3 and Figure 8). Because of the interannual variations in copepod developmental conditions, the exact boundaries of these zones may vary from one year to the other.

Zone 1 comprises subarctic open water, specifically the Norwegian Sea (Figure 8, blue dots). This region is heavily influenced by the inflow of warm Atlantic waters and has only one major spring bloom event. Because of warmer water temperatures and adequate phytoplankton food during the spring bloom, the critical development time is typically less than 45 days (Figures 7a and 7b). The open water *C. glacialis* population has a 1–2 year life cycle [Broms et al., 2009]. It is likely that C4 diapausers may continue maturing to C5 and adulthood within the first year.

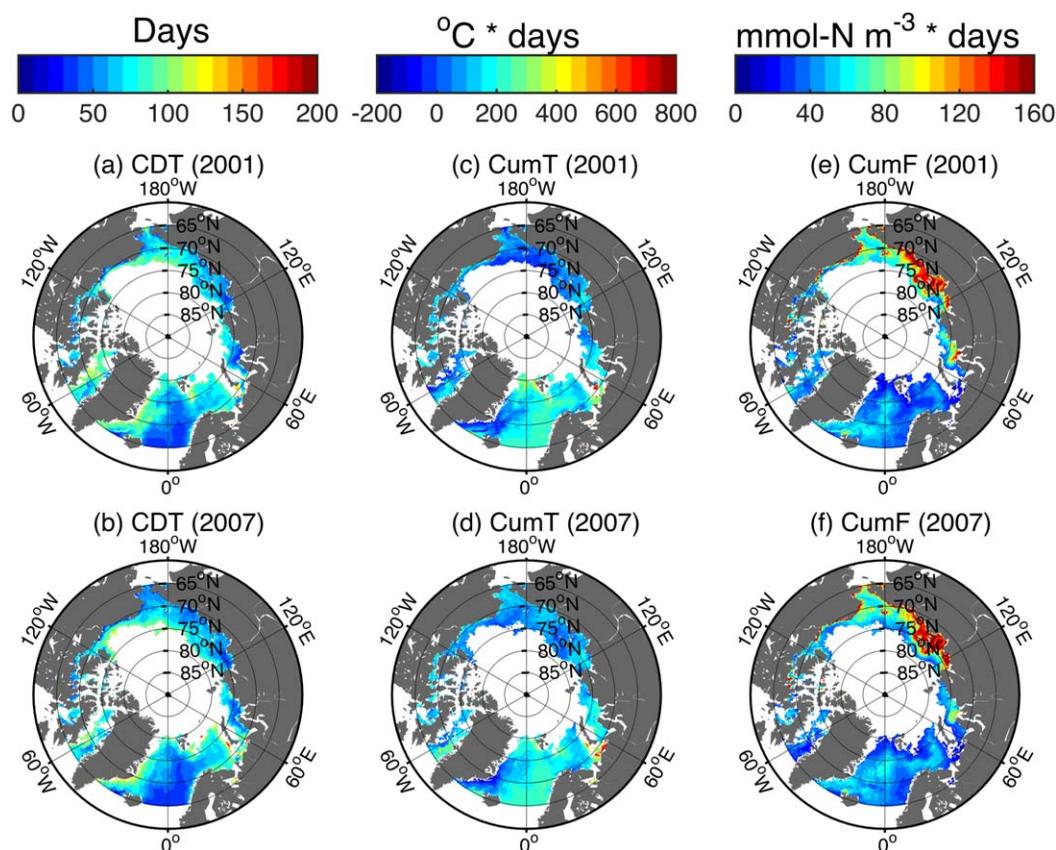


Figure 7. Critical development time (CDT), cumulative temperature (CumT), and cumulative food (CumF) of *C. glacialis* C4 diapausers in the baseline runs. The cumulative temperature (or food) is calculated by integrating diapausers' daily temperature (or food) model outputs over the entire critical development time. All individuals are positioned at their release locations.

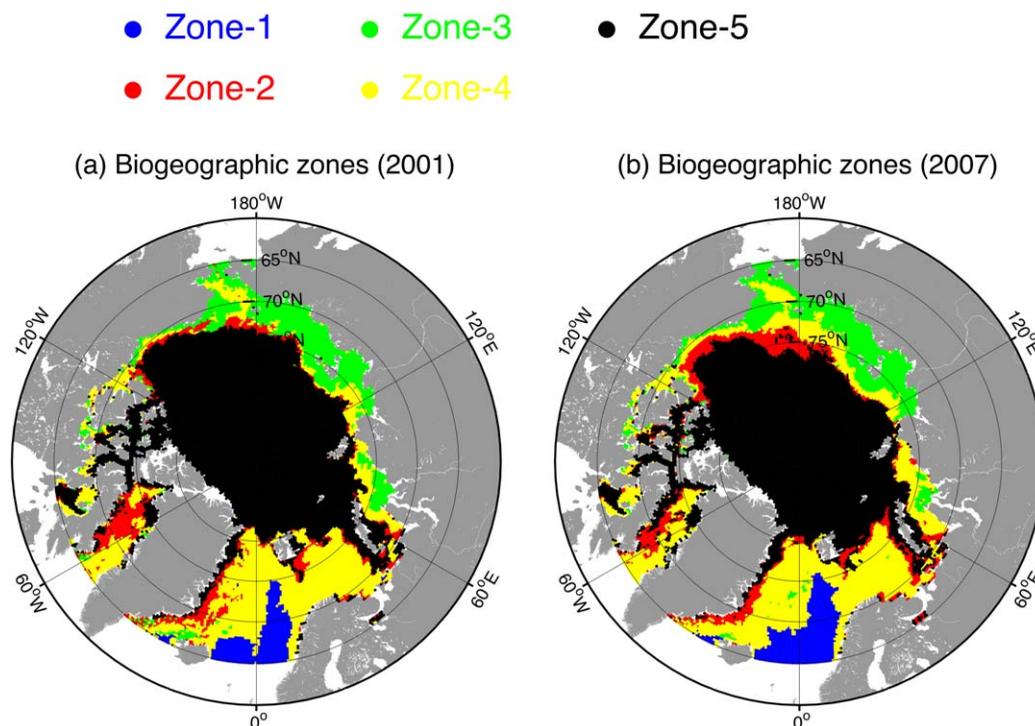


Figure 8. Five typical biogeographic zones summarized from the baseline runs in (a) 2001 and (b) 2007. All individuals are positioned at their release locations.

Although reproduction of a second generation late in the season is possible under favorable food conditions, that new generation may not have enough time to develop to C4 and diapause before winter [Wold *et al.*, 2011].

Zone 2 is a transitional zone between *C. glacialis* habitats and unsuccessful regions, and mainly includes outer slope seas to the margins of the central Arctic, Baffin Bay, East Greenland Shelf, and northern Barents Sea (see Figure 8, red dots). These regions have long-lasting ice cover, low water temperature, and a summer phytoplankton bloom. Therefore, *C. glacialis* there has a critical development time longer than 90 days (Figures 7a and 7b) and follows a typical 2–3 year life cycle [Conover, 1988; Kosobokova, 1999].

Zone 3 consists of shallow shelves in the Beaufort, Chukchi, East Siberian, Laptev, and Kara Seas (see Figure 8, green dots). These regions are characterized by intensive summer phytoplankton blooms after ice breakup (Figures 7e and 7f). With an abundant food supply, the critical development time of *C. glacialis* is primarily temperature-dependent and may vary greatly from one shelf to the other and interannually (Figures 7a and 7b).

Zone 4 contains other *C. glacialis* habitats that are highly variable in critical development time, temperature, and food, such as Greenland Sea, Barents Sea, Kara Sea, and Baffin Bay (see Figure 8, yellow dots). The critical development time varies between 45 and 90 days, and the cumulative temperature and food are also highly variable (Figure 7).

Zone 5 is the unsuccessful territories for *C. glacialis* development, primarily the central Arctic basins and northern Canadian Arctic Archipelago (see Figure 8, black dots). These regions typically have almost year-round ice cover, very low water temperature, and low, and thus inadequate, phytoplankton food. Successful recruitment and sustainable population development is unlikely, although low abundances have been observed that probably were advected from the adjoining shelf and slope seas [e.g., Ashjian *et al.*, 2003; Olli *et al.*, 2007; Kosobokova and Hirche, 2009; Kosobokova and Hopcroft, 2010].

4. Discussion

Our modeling study of *C. glacialis* life history development demonstrated that ocean warming and early ice retreat could potentially benefit this endemic copepod species and permit northward expansion of its

biogeographic boundaries, assuming that *C. glacialis* individuals match their development to the period of abundant food supply. Our results also suggested that sufficiently long growth seasons, during which food is adequate for life stage development, are critical to the developmental success of *C. glacialis* individuals, especially those in the northern limit of this species' biogeographic distribution.

4.1. Sea Ice Algae as Early Food for Copepod Reproduction and Development

Prior field studies have all suggested the importance of sea ice algae as early and critical food for copepod reproduction and development [e.g., Søreide *et al.*, 2010; Leu *et al.*, 2011; Wold *et al.*, 2011; Durbin and Casas, 2014]. Søreide *et al.* [2010] showed a close coupling between ice algal and phytoplankton blooms and reproduction success and growth of *C. glacialis* in a northern Svalbard fjord during the spring and summer seasons of 2007. In the same fjord, Leu *et al.* [2011] compared extensive observations in two consecutive years with distinctive ice regimes and suggested that relatively early ice breakup in 2007 resulted in a timing match scenario between two primary production blooms and secondary production (reproduction and growth) by *C. glacialis*, whereas late ice breakup in 2008 led to a timing mismatch and consequently a five-fold lower biomass of *C. glacialis*.

Based on our comparative model runs with and without ice algae (Figures 4a and 4b versus Figures 5g and 5h), the differences in *C. glacialis* distribution patterns seemed insignificant, and in many regions early food resulting from released ice algae did not substantially improve success in developing to diapausers. Nevertheless, ice algal food might be indeed critical to the individuals in the transitional zone (Zone 2 in Figure 8) because of their long critical development time. Those individuals must take full advantage of the early period of the growth season during which released ice algae dominate pelagic phytoplankton in the water column, otherwise they could not develop into C4 diapausers by the end of the growth season (see blue dots in Figures 5g and 5h).

4.2. Copepod Adaptation to the Arctic Environments

The widespread distribution of *C. glacialis* diapausers in the food-seeking runs suggests that adaptive behaviors increase *C. glacialis* fitness to the less suitable environments, such as in the central Arctic basins with low temperature and food and short growth season. Such strategies would allow this species to populate territories where they would otherwise be unsuccessful (green dots in Figures 5c and 5d). However, this species is not found in high abundance in those regions. The relatively low food levels in the central Arctic basins would probably restrict egg reproduction of *C. glacialis*, which has been shown to be dependent on available food [Hirche and Kattner, 1993; Plourde *et al.*, 2005; Madsen *et al.*, 2008; Kjellerup *et al.*, 2012], and hence limit recruitment and population growth in the central Arctic despite adaptive behaviors (such as migration to layers of food). Food-dependent egg reproduction rate was not parameterized in present model setting and was beyond the scope of the present study.

4.3. Ecological Implications of Ocean Warming and Sea Ice Reduction to Endemic Copepod Recruitment

Elevated ocean temperatures resulting from climate change is hypothesized to be associated with increased growth, development, and production rates and with changes in species distributions and biogeography in the Arctic Ocean [e.g., Wassmann *et al.*, 2011]. Examples of these effects have been reported from field studies as well as model simulations. In the White Sea (Russia), increases in abundance and earlier annual appearance of *C. glacialis* C1 have been linked to long-term warming of the upper 10 m since the 1960s [Usov *et al.*, 2013]. A coupled hydrodynamic-ice-ecosystem model study investigated Arctic primary and secondary production under 2–8°C atmospheric warming and concluded that the Arctic mesozooplankton species, exemplified by *C. glacialis*, could dramatically increase productivity in the Chukchi and East Siberian Seas and might expand to the Arctic basins under warming scenarios [Slagstad *et al.*, 2011]. The IBM study by Ji *et al.* [2012] demonstrated that a 2°C increase in water temperature would greatly expand the regions of successful *C. glacialis* diapausers northward based on temperature-dependent-only life history development.

The present study may provide a more comprehensive view of this endemic species' biogeographic boundary shifts under ocean warming than previous modeling efforts because it includes food dependency. Comparisons of successful diapausers in two contrasting years showed that the greater warming (on average 1–2°C warmer than 2001) and reduction of sea ice extent in 2007 might favor *C. glacialis* recruitment in

the marginal ice zones between the Beaufort, Chukchi, East Siberian, and Laptev Seas and the adjacent basins, and might allow *C. glacialis* diapausers to colonize regions in which they would be unsuccessful in the cold year (see magenta dots in Figure 4c red fan zone). Nevertheless, *C. glacialis* individuals were unsuccessful in developing to diapausers over much of the central basins (Figure 4), except in the simulations including active seeking for optimal food conditions (Figures 5c and 5d) or without food limitation (Figures 5e and 5f). This suggests that food is a predominant limiting factor for *C. glacialis* population recruitment in the central Arctic. Despite field observations of *C. glacialis* aggregation near the chlorophyll maximum (food seeking), they are not believed to recruit in the central Arctic as shown in the model results (Figures 5c and 5d), suggesting that on average over their development periods, *C. glacialis* in the field does not experience optimal food availability and may not always exploit the optimal food conditions. Alternatively, BIOMAS forcing could overestimate water column ice algae/phytoplankton biomass concentrations that are then used in the ArcIBM simulations, although this seems unlikely since BIOMAS has been shown to underestimate phytoplankton concentrations in some regions [Zhang *et al.*, 2010].

In the central Arctic basins, due to a lack of nutrient, primary production is projected to remain low or to slightly increase from present low-productivity regime in the next few decades, even if sea ice continues to diminish and light availability significantly increases [Wassmann and Reigstad, 2011; Lawrence *et al.*, 2015; Slagstad *et al.*, 2015; Yool *et al.*, 2015]. Physical constraints (e.g., stratification) and nutrient limitation appear to also limit secondary production (*C. glacialis*) in the future central Arctic, as shown by the ecosystem model experiments forced by Intergovernmental Panel on Climate Change (IPCC) climate projections [Slagstad *et al.*, 2015]. Central-basin *C. glacialis* individuals may remain unsuccessful in their life history development because phytoplankton food would still be a limiting factor for their potential colonization in the near future.

In the Arctic shelf/slope seas, continuing warming and sea ice loss may disrupt the timing of several key processes (e.g., earlier ice retreat, shorter ice algal growth season, and earlier onset of the pelagic phytoplankton bloom) and also change both the quantity and quality of the food. The potential timing mismatch between *C. glacialis* and its algal food may have a negative impact on its reproduction, growth, and population persistence [Søreide *et al.*, 2010; Leu *et al.*, 2011]. Our model designs, releasing egg or N3 individuals at the onset of the phytoplankton bloom so that development initiates when food is available, presented a best-case scenario for *C. glacialis*. A mismatch between ice algae and water column phytoplankton blooms and *C. glacialis* life stage development that reduced the length of the growth season or the cumulated available food relative to these best-case scenarios would only reduce the regional extent over which *C. glacialis* could attain diapausing stages.

4.4. The Roles of Temperature and Food that Cause *C. glacialis* Boundary Shifts

Because of the high nonlinearity in the temperature- and food-dependent development relationship (see equation (3)), it is difficult to disentangle which factor (temperature or food) is more important in shifting *C. glacialis* biogeographic boundaries from a pan-Arctic perspective. To address this, 583 individuals that succeeded in 2007 but that failed in 2001 from the Pacific Arctic seas (see magenta dots in Figure 4c red fan zone) were further analyzed. In 2001, the average critical development time of these failed individuals was 150 days, much longer than the average growth season length of 91 days (Figures 9a and 9b). In 2007, however, the average critical development time of the same but successful individuals was reduced to 73 days, whereas the growth season length was protracted to 108 days (Figures 9a and 9b). Also, the mean and cumulative temperature and food were all higher in 2007 than in 2001 (Figures 9c–9f). These differences suggested that the shortened critical development time (mainly due to ocean warming) and prolonged growth season (due to earlier ice retreat and more available food) in 2007 allowed those individuals to develop from egg to past midway C4 within that year. Increases in temperature and food availability both contributed to the greater northward expansion of *C. glacialis* diapausers in 2007 relative to 2001, although warming might play a more significant role in expanding diapausers poleward in the Pacific Arctic shelf/slope seas.

4.5. Model Limitations and Future Directions

Although the simulations in the present study yielded greater insight into the factors regulating the development of this key species and how the water temperature and food environments may define its biogeographic distribution in the Arctic Ocean, the work showed both some limitations to the modeling as well as

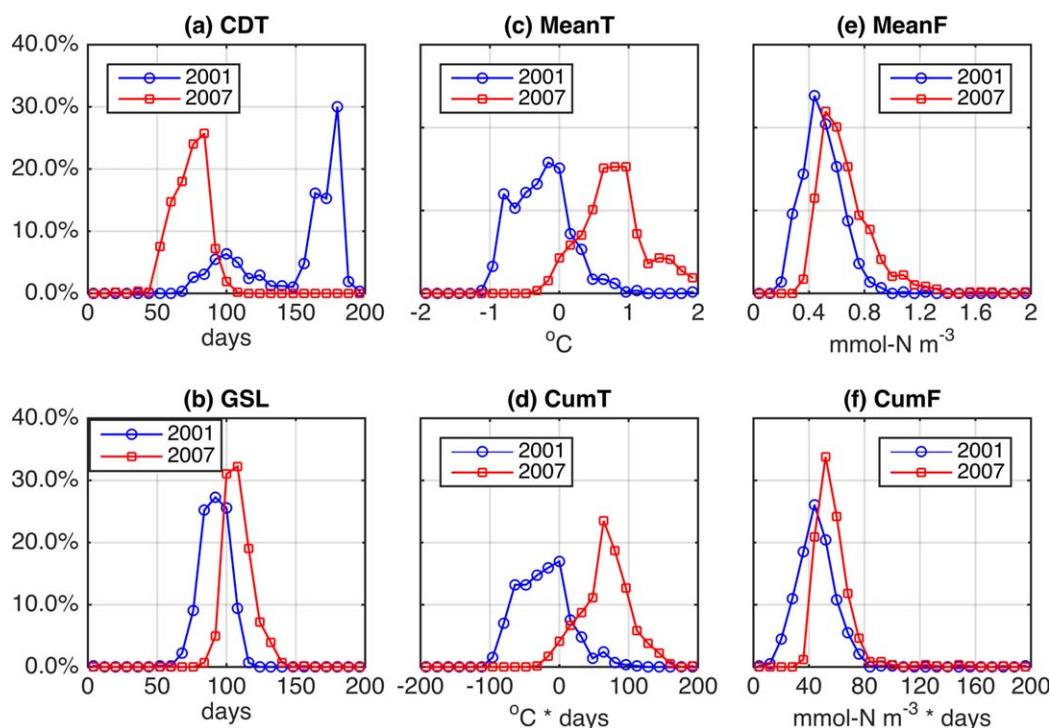


Figure 9. Frequency distributions of (a) critical development time (CDT), (b) growth season length (GSL), (c) mean temperature (MeanT), (d) cumulative temperature (CumT), (e) mean food (MeanF), and (f) cumulative food (CumF) for 583 *C. glacialis* individuals that successfully developed to diapausers in 2007 but that failed in 2001 in the Pacific Arctic seas (magenta dots inside Figure 4c red fan zone).

suggested future directions of inquiry. The modeling was limited in which it addressed only very specific questions and was confined only to investigating the interplay between temperature- and food-dependent development, environmental conditions, and circulation. The modeling also depended critically on both water temperature and food availability from the BIOMAS ice-ocean-ecosystem model. Although that model has been validated against field observations [Zhang *et al.*, 2010, 2014, 2015], it is possible that some aspects of timing and magnitude may not be entirely accurate. Observation data from field studies, especially many biological variables, are available only sparsely in time and space, making model validation and improvement difficult. Nonetheless, both the BIOMAS modeling and our ArcIBM modeling provide valuable opportunities to explore the factors driving and shaping Arctic ecosystems and the copepod biogeography.

Future directions for inquiry include thermal physiology and mortality in the changing Arctic environment. Changes in water temperature will impact not only zooplankton development rate, but may also have physiological consequences, most notably thermal tolerance and energy balance. Alcaraz *et al.* [2014] experimentally determined the carbon-specific ingestion and respiration of *C. glacialis* under a variety of controlled temperatures and concluded that 5–6°C is the upper thermal threshold for this species. Another potential physiological response to temperature is diapause initiation based on observational evidence from the White Sea [Kosobokova, 1999] and a subarctic fjord in western Norway [Niehoff and Hirche, 2005] that showed increasing temperature in the surface water appeared to force *C. glacialis* to descend to deeper waters, to diapause if the diapausing stage had been achieved, even though food conditions were still adequate in the upper ocean. Exploring the thermal physiological responses of individuals and populations would require more sophisticated trait-based modeling of zooplankton development, growth, and migration (e.g., age/stage, body mass, and lipid content) and the implementation of life history strategies and decisions (e.g., capital versus incoming breeding, egg reproduction timing and rate, and diapause entry and exit) [Varpe *et al.*, 2007, 2009; Ji, 2011; Maps *et al.*, 2012, 2014; Record *et al.*, 2013].

The causes and extent of mortality of *C. glacialis* and other plankton in the Arctic still remain poorly understood and quantified [Daase *et al.*, 2014], making it difficult to incorporate this important driver into modeling efforts and to approach questions regarding species distributions and biogeography from a top-down

control perspective. In one study, *Berge et al.* [2012] argued that predation pressure by baleen whales was a driving force in structuring Arctic *Calanus* communities but such demonstration and quantification of mortality in the field is rare. An additional aspect is related to the Arctic lightscape as continuing reductions in snow and sea ice cover would increase the amount of light available to visual predators (e.g., fish) that would increase predation pressure on zooplankton in the future (i.e., negative feedback from climate change) [*Varpe et al.*, 2015].

5. Conclusions

The major findings of this pan-Arctic *C. glacialis* life history modeling study were (1) *C. glacialis* could expand its northern boundaries from the Arctic shelf/slope seas to the fringe of the central basins in a low sea ice year (e.g., 2007) with earlier ice retreat, warmer temperature, more available food, and longer growth season, assuming *C. glacialis* could match its life stage development to the period of adequate phytoplankton food. (2) Due to long critical development time, *C. glacialis* individuals residing in the transitional zones between successful and unsuccessful territories may be the most susceptible to the interannual variability of environmental conditions, reproduction timing, and availability of ice algal food. (3) Food availability is a major limiting factor for *C. glacialis* development in the central Arctic basins, while increasing temperature may play a more important role in expanding *C. glacialis* diapausers poleward in the Arctic shelf/slope seas.

Acknowledgments

Discussions with Øystein Varpe (UNIS), Yun Li (USF), and Stephen Elliott (MIT-WHOI joint program) helped model experimental design and result interpretation. We thank joint program student Benjamin Jones for his assistance in modifying model code and setup. The original IBM source code was developed by Geoffrey Cowles (UMass-Dartmouth). This work was funded by the National Science Foundation Polar Programs (grants PLR-1417677, PLR-1417339, and PLR-1416920). Two anonymous reviewers provided constructive comments. Upon publication, the ArcIBM model data will be available from a Woods Hole Oceanographic Institution web server (http://delmar.whoi.edu:8080/thredds/catalog/default/Early_Ice_Retreat_Exp_REVISION/catalog.html).

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